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The Orb-Weaver Genus *Mecynogea*, the Subfamily Metinae and the Genera *Pachygnatha, Glenognatha* and *Azilia* of the Subfamily Tetragnathinae North of Mexico (Araneae: Araneidae)

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THE ORB-WEAVER GENUS *MECYNOGEA*, THE SUBFAMILY METINAE AND THE GENERA *PACHYGNATHA, GLENOGNATHA* AND *AZILIA* OF THE SUBFAMILY TETRAGNATHINAE NORTH OF MEXICO (ARANEAE: ARANEIDAE)

HERBERT W. LEVI[1]

ABSTRACT. Several genera are desribed and illustrated, webs are pictured when known, and distributions are plotted. These genera include: *Mecynogea* with one species, *Nephila* with one, *Leucauge* with two, *Metellina* with three, *Meta* with two species (one of them new, from California caves, similar to a Mediterranean cave *Meta*), the new genus *Metleucauge* with one new North American species (others in eastern Asia), *Pachygnatha* with eight species, *Glenognatha* with two and *Azilia* with one North American species.

On the basis of numerous characters, it appears that Metinae is the primitive group, with the greatest number of plesiomorph characters, Tetragnathinae are specialized in one direction, Araneinae in another. Because of the numerous intermediate genera, it is best to combine the family Tetragnathidae with Araneidae, but to consider the group a subfamily.

INTRODUCTION

Hope of learning about the relationships among orb-weavers was the reason for combining revisions of diverse orb-weavers in this paper. The only genera of the Tetragnathinae not included here are *Dolichognatha* and the large genus *Tetragnatha*. No surprising discoveries were made, but evidence was provided in support of the classification of 19th century arachnologists.

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RELATIONSHIPS

One of the purposes of this revision was to learn about the relationships of *Meta* and *Tetragnatha*. It was for this reason that *Meta* and *Pachygnatha* and their relatives were revised together. *Mecynogea* was first thought close to *Meta*. It is clear now that it belongs to the Araneinae.

The characters that were chosen for studying relationships are the following (Table 1):

1. *Eye placement.* In *Meta* the median eyes are within their diameter of each other and about two diameters at most from the laterals. The laterals touch each other. This condition is found in *Meta* (Fig. 112), *Pachygnatha* (Figs. 163, 165) and also in *Zygiella* (revised previously) and various small-sized Araneinae, as well as in Linyphiidae and Theridiidae. It is believed the primitive condition of Araneoidea. The lateral eyes have further separated from the medians in many specialized Araneidae, e.g. *Araneus diadematus* and female *Nephila* (Fig. 34).

The lateral eyes are rarely separated. Separated lateral eyes are characteristic of *Azilia* (Fig. 294, 300) and *Tetragnatha* (and some genera not found in the north temperate region). It is possible that this is the ancestral condition, since uloborids and many other families have lateral eyes separate.

2. *Eye structure.* The canoe tapetum is characteristic of the Araneoidea. It is found in *Meta* and relatives, *Zygiella*, *Nephila* and in the lateral eyes of *Pachygnatha*.

In Araneidae there are two differences. First, in all genera close to *Araneus* (that is, in most nearctic genera previously revised), the canoe tapetum of the posterior median eyes has shrunk, and the rhabdoms are arranged in looping rows toward the median (of the spider) (Fig. 11). In *Argiope* this condition is also found in the lateral eyes. Secondly, in the posterior eyes of *Pachygnatha* the tapetum has disappeared, and the eye is filled with looping rows of rhabdoms (Figs. 157, 161) which may resemble a maze (Fig. 159). In *Azilia* and *Tetragnatha* the tapetum has been lost in all secondary eyes, and in *Azilia* the rhabdoms are arranged in neat rows which turn at their ends (Figs. 299, 300). This is without doubt an improvement in eye structure (Homann, 1971), as it is accompanied by larger optic centers in the brain. But it is strange that a twilight and cave spider, *Azilia*, has lost the tapetum. *Glenognatha emertoni* has eyes like those of *Pachygnatha* with no canoe tapetum in the posterior median eyes; but here the cells in the rows of rhabdoms have a tapetum (Fig. 262).

The shrunk tapetum is found in that group of spiders with complicated palpi (see below) having many palpal sclerites. The tapetum is absent in those spiders in which the few palpal sclerites present have become modified. Therefore, it is believed that evolution went in two different directions from the more generalized *Meta* eyes.

3. *Trichobothria.* It is characteristic of the superfamily Araneoidea to have few leg trichobothria, and one diagnostic feature is the lack of trichobothria on tarsi where their presence might interfere with touching and measuring silk strands. In general there are trichobothria only on the dorsum and sides of tibiae, and usually there is one on the proximal half of the metatarsus (some Linyphiidae have more elaborate patterns of trichobothria). Specialized trichobothria are found on the third tibia of *Mangora*; they are very long, feathered and of unknown function. Also the fourth femur of *Leucauge* has

very fine, long trichobothria of unknown function (Figs. 50, 51). *Leucauge*, *Pachygnatha*, *Glenognatha* and *Tetragnatha* have several trichobothria dorsally at the proximal end of the femur, which is perhaps a specialization. Perhaps the presence of femoral trichobothria in Uloboridae indicates a hitherto unexplored relationship with *Tetragnatha*. In some adult *Pachygnatha*, spiders that make no webs, the trichobothrium has moved to the distal end of the metatarsus, a unique change.

4. *Male palpi.* The simplest palpi in Araneoidea are found in some theridiids (Levi, 1961) and in *Metellina* and *Leucauge*. The *Metellina* and *Leucauge* palpus has only a (spherical) tegulum with subtegulum and basal hematodocha, and bearing on the distal end an embolus held by the conductor (E, C in Fig. 59). The only specialized structure in the *Metellina* palpus is the elaborate paracymbium (P in Fig. 124).

The palpus has become specialized in two different ways: 1) Some species have acquired numerous sclerites. This is foreshadowed in *Metleucauge* (Fig. 149). However in *Araneus* and most relatives the bulb twists in such a way that the sclerites move from the tip of the bulb to the side facing the median. Also the folded hematodocha and tegulum face laterally (Figs. 13, 14). These modifications are characteristic of the relatives of *Araneus*; I do not know of any other group of spiders in which they are seen. *Zygiella* is intermediate: the tegulum has moved laterally, the embolus is still distal in both Z. *x-notata* and Z. *thorelli*. 2) In other genera the cymbium shrinks, the paracymbium becomes a separate sclerite, and embolus and conductor become more complicated structurally. This palpus is found in *Pachygnatha* (Fig. 177) and *Tetragnatha*.

5. *Female genitalia.* In *Meta* and *Metellina* the openings into the seminal receptacles are so close to the genital groove that the duct into the seminal receptacles may also be the fertilization duct. Wiehle (1967) described this and called it the semientelegyne condition. I am not certain this is correct; there might be two openings with adjacent ducts (Figs. 116, 120). In other Araneoidea, the two ducts (connecting and fertilization) always originate (or end) together on the seminal receptacles; when they are very short it may be difficult to tell whether one or two ducts are present. Again, there are two specializations: 1) The seminal receptacles move anteriorly, the epigynal openings may still only be slits on the posterior face of the base of the epigynum (e.g. *Araneus diadematus*, *Eriophora*). Characteristic of this group, related to *Araneus*, is the annulate scape. The scape is not always present but has been lost in heavily sclerotized species (e.g. *Mastophora*, *Gasteracantha*, Levi, 1978c); it is also absent in *Mecynogea* (Fig. 1). It is of interest that some species of *Zygiella* have a scape. (These species belong to *Zygiella* due to the canoe-shaped eye tapetum and to a ventral apophysis or modifications of the tegulum of the palpus, the latter a unique synapomorphy found in most members of the genus.) 2) The second direction is the (perhaps) secondary loss of the epigynum. In *Pachygnatha* the anterior ventral cover of the epigynum grows posteriorly over the posterior ventral cuticle and forms two chambers: a posterior chamber whose dorsal wall is the ventral cuticle which retains the same setae pattern inside the chamber as outside (Figs. 182, 194). And there is an anterior chamber with the seminal receptacles on each side at the posterior edge. There appears to be a connecting duct from the posterior chamber into the seminal receptacles and a fertilization duct from the receptacles to the anterior chamber. The anterior chamber appears open in the middle toward the posterior one. This looks surprisingly similar to the *Meta* sections made and structures shown by Wiehle (1967, fig. 31). Of course this might be considered primitive. Further evidence

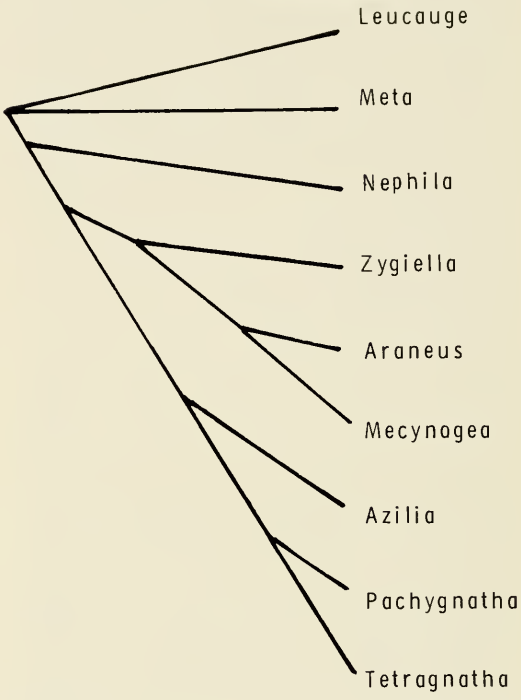
TABLE 1. CHARACTER STATES OF 11 GENERA: + PRESENT AND BELIEVED SPECIALIZED (APOMORPH); − NOT PRESENT AND BELIEVED PRIMITIVE (PLESIOMORPH); ± PRESENT IN SOME SPECIES. *Abbreviations.* L, left; LE, lateral eyes; M, median apophysis; PME, posterior median eyes; R, right; SR, seminal receptacles.

Presumed derived character state	*Araneus*	*Mecynogea*	*Zygiella*	*Nephila*	*Leucauge*	*Metellina Meta Metleucauge*	*Pachygnatha*	*Azilia*	*Tetragnatha*
1a lateral eyes distant from medians	±	−	−	+ in ♀	−	−	−	−	±
b lateral eyes separated	−	−	−	−	−	−	−	+	±
2a PME without canoe tapetum	−	−	−	−	−	−	+	+	+
b LE without canoe tapetum	−	−	−	−	−	−	−	+	+
c specialized canoe in PME	+	+	−	−	−	−	−	−	−
3 short trichobothria on femur	−	−	−	−	+	−	+	−	+
4a ♂ palpi with M	+	?	±	−	−	−	−	−	−
b large paracymbium	−	−	+	−	−	+	+	−	+
c paracymbium separate	−	−	−	−	−	−	+	−	+
d sclerites face mesally	+	+	±	−	−	−	−	−	−
e dissected cymbium	−	−	−	−	−	−	+	−	+
5a epigynum absent	−	−	−	−	−	−	+	−	+
b SR not sclerotized	−	−	−	−	+	−	−	+	−
c scape present	+	−	±	−	−	−	−	−	−
6 mating spiders do not separate between R and L palp use	−	?	−	?	?	−	+	?	+
7 clypeus low	+	+	+	+	+	+	−	+	+
8 ♂ chelicerae large, used in mating	−	−	−	−	−	±	+	−	+
9 ♂ coxal hook, 1st or 2nd leg modified for mating	+	−	−	−	−	−	−	−	−
10 ♂ endite with lateral tooth	+	−	−	−	−	−	−	−	−
11 labium wide	+	+	+	−	+	+	+	+	+
12a endites distally wide	−	−	−	−	−	±	+	+	+
b endites square	+	+	+	−	−	−	−	−	−
13 orb-web without open hub	+	+	+	+	−	−	−	+	−

Table 1. Continued.

Presumed derived character state	*Araneus*	*Mecynogea*	*Zygiella*	*Nephila*	*Leucauge*	*Metellina* *Meta* *Metleucauge*	*Pachygnatha*	*Azilia*	*Tetragnatha*
14a tetragnathid silk measuring	−	−	−	with 4th leg	+	+	−	+	+
b araneid silk measuring	+	+	?	with 4th leg	−	−	0	−	−
15 bulky ventral cecae	+	?	+	?	−	+	−	?	−
16 femora stretched when resting	−	−	−	+	+	+	+	?	+

Table 2. Cladogram obtained by Wagner tree analysis of the data in Table 1 using the computer program "Wagner 78" developed by J. S. Farris (a later version of Farris, 1970). All characters are weighed equally (minuses avoided, no zero, pluses arbitrarily 2's, variable characters as intermediate 1's). Prepared by M. Stowe.



that the loss of the epigynum is secondary is the presence of an epigynum in the related *Azilia* (Fig. 291) and *Dolichognatha* and the fact that in copulation only one male palpus is used at a time. In *Meta* and spiders with epigynum, palpi are alternated; in haplogyne spiders two palpi are used simultaneously (Gerhardt, 1921).

6. *Mating behavior.* The diversity of reproductive organs suggests investigating mating behavior. Male spiders of the haplogyne families use the two palpi simultaneously: the male's left palpus enters the right side of the genital opening, the right palpus enters the left side when the spiders mate facing each other. If tetragnathids are really haplogyne, one would expect a similar copulation. This how-

ever is not the case. Male theridiid and linyphiid spiders mate by alternating left and right palpi. The left is introduced in the left side of the epigynum, the right into the right side (Gerhardt, 1921). Gerhardt describes the copulatory behavior of various araneid genera. *Argiope* and all those species related to *Araneus* mate twice only. After mating once with one palpus, they separate and court again before using the second palpus (Gerhardt, 1926). (Gerhardt found it remarkable that the males of species now placed in *Nuctenea* and some others can mate three to four times. We now know that, unlike *Araneus* or *Hypsosinga* species, no sclerite breaks off the palpus in *Nuctenea* to prevent further copulations.) *Meta* is described by Gerhardt as using only one palpus, after which the pair separates (Gerhardt, 1927). *Nephila maculata* mates with one palpus before separating, then uses the other after a second courting (Robinson, personal communication). *Pachygnatha* uses one palpus for one hour at a time before separating (Gerhardt, 1921). The length of mating time is unique for *Pachygnatha*; it is only minutes in *Zygiella*, *Meta* and *Tetragnatha*. In *Tetragnatha* each insertion is 5 to 7 minutes, and within half an hour the palpi alternate (Gerhardt, 1921). Here *Meta* and *Araneus* species share a behavior which is perhaps primitive and closer to that of haplogynes, while tetragnathids eventually alternate palpi, approaching the perhaps more specialized behavior of theridiids and linyphiids. Unlike *Araneus* but like haplogynes, *Tetragnatha* in sperm induction use both palpi together (Gerhardt, 1927).

7. *Clypeus.* The clypeus is high (more than twice the diameter of the anterior median eyes) in most Araneoidea. The clypeus is low in *Metellina* and *Leucauge* (Figs. 47, 72), and in most relatives of *Araneus* (but not all, e.g. *Kaira*, *Scoloderus*). The clypeus is high in *Pachygnatha* (Fig. 162). Is this high clypeus secondary (as perhaps in *Scoloderus*) or is it a primitive condition? The high clypeus of *Kaira* and *Scoloderus* certainly does not indicate relationship with *Pachygnatha*.

8. *Chelicerae.* Chelicerae of *Metellina* and *Leucauge* (Figs. 54, 72) are like those of other Araneoidea, but probably weaker and more generalized than those of *Araneus*, and possess only a slight proximal boss. *Araneus* relatives have a proximal boss, as do the enlarged chelicerae of *Pachygnatha*.

The enlarged chelicerae of the adult, especially adult males, are characteristic of *Tetragnatha*, *Pachygnatha* (Figs. 163, 166) and *Dolichognatha*, but not of *Azilia*. The large chelicerae couple when the animals mate. Enlarged chelicerae are also found in *Metellina curtisi* males (Fig. 73). The enlarged male chelicerae are a specialization. They are most modified in *Pachygnatha* and *Tetragnatha*.

9. *Legs.* In contrast, in *Araneus* and many related genera the sexes couple with legs. The first coxae of males have a hook that fits into a slit on the second femur. The legs of males are frequently modified in other ways, but not in the genera described in this paper. I believe the modifications of coxae and legs to be specializations, synapomorphies of the genera close to *Araneus*. (However, *Azilia* males have stronger macrosetae on legs than females.)

10. *Endite tooth.* An unusual modification found in males of *Araneus* and related genera (not in any of the genera considered here) is the lateral tooth on the endite (gnathocoxa), facing a tooth at the proximal end of the palpal femur. I consider the endite tooth and the one on the palpal femur synapomorphies of the *Araneus* group of genera.

11. *Labium.* The labium is longer than wide in most haplogyne spiders, probably a primitive condition. A long labium is found in *Nephila* (Fig. 24); in all other genera of Araneidae and Tetragnathinae examined, the labium is wider than long.

12. *Endites.* Endites (gnathocoxae) of haplogynes are usually longer than wide, perhaps a primitive condition. Of course most mygalomorph spiders do not have pedipalpal coxae with endites. *Meta* have long endites which I believe to be the primitive type (Fig. 121). Endite form also appears to have specialized in two different directions. In *Leucauge* (Fig. 53), *Metleucauge* (Fig. 144), *Pachygnatha* (Fig. 153) and *Tetragnatha* the endite is distally wider than proximally, a synapomorphic state. Perhaps the long endites evolved with the elongated chelicerae. The endite of *Araneus* and relatives is as wide as long, very heavy (Fig. 6; Levi, 1968, fig. 65), a specialization in another direction. The *Nephila* endite is heavy, widest near the tip of the labium (Fig. 24). The long endites of *Metepeira* are unusual for a genus otherwise close to *Araneus*.

13. *Orb-webs.* Studies of araneoid orb-webs have been of surprisingly little help in providing data for phylogenetic studies (Levi, 1978a, 1978b). Apparently, araneoid webs, the design of which is important in determining the kinds of prey captured, have undergone frequent and diverse evolutionary changes as a result of strong competition for prey (Levi, 1978b). Adult *Pachygnatha* species have no webs; close relatives in *Glenognatha* do. *Tetragnatha* and all *Meta* relatives have a loose web with an open hub, perhaps a synplesiomorph condition. The web of *Nephila* is believed specialized (Plate 2) and is quite different from that of the related *Nephilengys* (M. Robinson, pers. comm.). The *Mecynogea* web is specialized: a dome that lacks viscid silk (Plate 1); and that of *Zygiella* lacks viscid silk in an upper sector of an orb. The webs of relatives of *Araneus* exhibit great diversity (Levi, 1978b).

14. *Silk handling.* An interesting character was recently found by Eberhard (in manuscript): species related to *Meta* and *Tetragnatha* measure webs one way; most species, all related to *Araneus*, measure another way; and *Nephila* measures with the fourth leg.

15. *Ceca.* The ventral intestinal ceca run only to the coxae of legs in *Araneus*, *Zygiella* and *Meta*. These genera have one bladder-like cecum in front of the dorsal apodeme (Palmgren, 1978). *Tetragnatha* and *Pachygnatha* have bulkier ventral ceca that extend into the chelicerae and the pedipalpal coxae, and have a posterior unpaired dorsal cecum behind the dorsal apodeme. *Leucauge* has ceca like *Tetragnatha* (Palmgren, 1979).

16. *Resting position.* Living specimens of *Leucauge* (Plate 3), *Metellina* (Plate 6) and even *Pachygnatha* (Plate 7) are similar and resemble *Tetragnatha*. They appear very different from *Larinia* (Levi, 1975, plate 1), another narrow, elongate spider that stretches out along twigs. Striking similarities between *Leucauge* and *Metellina* are the lack of strong setae, the curved metatarsi, and most important, the forward resting position of the first and second femora. The first and second femora are always held backwards, femoral-patellar joint flexed, in the resting position of Araneinae (Levi, 1975, plate 1). The resting position of uloborids in the web is like that of *Leucauge* and *Meta*.

Holding the anterior legs pulled in, in the Araneinae, may be the primitive condition, as it is the more widespread posture in the Araneoidea; projecting femora would represent a specialized posture. Since the pulled-in legs permit only small clearance between the leg articles for the lateral eyes to function, the lateral eyes touch each other. The great distance of the lateral eyes from medians in many Araneinae is no doubt an adaptation to this resting position, making it easier for the laterals to function. The separation of the lateral eyes in *Azilia* and many Tetragnathinae is made possible by the resting position: the anterior legs stretch forward, leaving the eyes a larger clearance in which to function.

17. *Silk glands.* Kovoor (1972) wrote that *Araneus* and *Argiope* have two kinds of aciniform silk glands, *Meta* and *Zygiella* [*Zilla*, sic] only one kind. Aciniform glands produce silk used in wrapping prey.

In summary, it appears that those genera close to *Meta* have most characters considered primitive (Table 1). Those of *Tetragnatha* and *Pachygnatha* are specialized in one direction, while those close to *Araneus* are specialized in another. This differs from previous conclusions regarding Tetragnathidae as the most primitive group.

CLASSIFICATION

One easy and fashionable solution to these phylogenetic problems is to declare that each one of the genera or groups of genera (Table 1) differs from the others and has to be placed in its own family. Unfortunately, this is not a useful method to solve the problems of relationship, and I prefer instead to place all in the family Araneidae (perhaps the other extreme). The family Araneidae can then be split into three subfamilies. But this division is not so clear-cut as that of families should be. The oldest name of the included family group name has to be used for each of these three taxa: Araneinae, Metinae, Tetragnathinae. Although Thorell (1869) and Simon (1894) discussed similar problems, more genera are now known and better understood than were known to them. Although closer to *Araneus* than to *Meta*, the following genera seem to be distinct: *Mangora, Argiope, Mecynogea* and *Cyrtophora. Nephila,* which is closer to *Meta* than to *Araneus*, may belong to a special group of the Metinae. This will be followed up in future research.

Subfamily Araneinae

Diagnosis. Secondary eyes with canoe tapetum, posterior median eyes with the canoe narrow and looping rhabdom rows toward the median of the spider (Fig. 11). Lateral eyes often some distance from medians. [*Cyclosa* is an exception to this eye morphology, but the eye description (Homann, 1971) may be in error.] Palpus with sclerites moved to median surface of bulb, the folded hematodocha and tegulum facing laterally (Figs. 13, 14). Paracymbium a small hook at cymbium base. The epigynum often has an annular scape. Males mate with one palpus at a time, the pair separating between copulations. Complete absence of trichobothria on femora. Chelicerae very strong with proximal boss. Endites short and square. Males often with hook on coxa one and with first or second legs modified to hold female when mating. In resting position first and second femora are directed posteriorly, the femoral-patellar joint flexed.

Comment. There are several genera which may be nuclei of subgroups: 1) *Gea* and *Argiope*; 2) *Mangora*; and 3) *Mecynogea* and *Cyrtophora.*

Subfamily Metinae

Diagnosis. Secondary eyes with canoe tapetum (Figs. 48, 49). Lateral eyes always close to medians (except in *Nephila*). Palpus usually very simple with embolus held by conductor, a spherical tegulum and subtegulum, other sclerites usually absent (Figs. 58, 59). Paracymbium often elaborate but attached to cymbium (Fig. 124). Epigynum very simple; fertilization ducts may be absent. Males mate with one palpus at a time, separating from female before using second. Endites long. Webs with open hub (Plates 4, 5, 6). Resting position with first and second femora extended forward (Plates 3, 6).

Comment. Kaston (1948) mentions lack of grooves on the sclerites above the book-lungs. I am not certain whether this is always so.

Zygiella is best placed with the Metinae, even though some species have a scape in the epigynum. The unique teg-

ulum of the male palpus of most species is evidence that those species with and without scape belong together. Also intermediate is the lateral position of the tegulum in the palpus. The embolus and conductor however are distal, not mesal. The leg resting position of *Zygiella* is like that of the Araneinae.

Nephila may belong in a separate subgroup or subfamily.

Subfamily Tetragnathinae

Diagnosis. Canoe tapetum lost in at least posterior median eyes (Figs. 157, 161, 300), usually lost in all secondary eyes (Fig. 299); rhabdoms arrange themselves in looping rows. Palpus similar to that of Metinae but cymbium reduced, and paracymbium usually a free sclerite (Fig. 177) (not in *Azilia*). Epigynum very simple or secondarily lost. After using one palpus repeatedly, the mating male alternates to use the other palpus. Endites long (Figs. 153, 257, 298). Trichobothria on base of femora (not in *Azilia*). Male chelicerae usually large, engaged with those of female when mating. Webs usually with open hub (not *Azilia*). The resting spider has the femora extended forward.

Comments. The genera *Pachygnatha*, *Azilia*, *Mimognatha*, *Glenognatha*, *Dolichognatha* and *Tetragnatha* belong here, but *Azilia* appears close to *Leucauge*.

RELATIONSHIP TO OTHER FAMILIES

The genera of Theridiidae closest to Araneidae are *Enoplognatha* and *Robertus* (and perhaps *Steatoda*). Both are closest to the Metinae because the bulb has not turned, as in Araneinae, and the cymbium is not modified, as in Tetragnathinae. The paracymbium is on the lateral edge of the cymbium, but not at the base. Both have a colulus. In other theridiids the paracymbium is a hook on the upper edge of the alveolus of the cymbium behind the bulb. Other genera also lack a colulus. Unlike *Meta*, the genera *Enoplognatha*, *Robertus* and *Steatoda* have diverse sclerites, radix and median apophysis in the palpus.

At the time I studied the Theridiidae, I presented a series from *Theridula* to *Enoplognatha* (Levi, 1961) showing the origin of various sclerites from the simple palpus, including the origin of the paracymbium from a hook behind the bulb (Levi, 1961, fig. 6). All the spiders with the simplest palpi lacked a colulus. I thought that the colulus, found in all other Araneoidea, was perhaps not a primitive structure at all, as postulated, and not a homolog of the cribellum. Evidence from Glatz (1973) indicates that the muscles of the cribellum do in fact correspond with those of the colulus even though *Uroctea*, closely related to *Oecobius* (Oecobiidae), lacks a colulus while *Oecobius* has a cribellum. Adult male uloborids may lack a cribellum as well as a colulus. Could neoteny explain the apparent paradox that the species with the simplest palpi lack this structure?

Characteristically all theridiids, with rare exceptions, have each chelicera drawn out proximally to a point hidden by the often transparent clypeus (Levi and Levi, 1962, figs. 9–21). This point, a place of muscle attachment, is missing in *Meta*, *Araneus* and *Linyphia* (Levi and Levi, 1962, figs. 23–28) and in the specialized theridiid chelicerae of *Dipoena* and *Euryopis* used for ant predation. But the drawn-out chelicerae are also present in some other araneoid families such as Mysmenidae and Nesticidae, and in the elongated chelicerae of *Mimetus* (Mimetidae). Only rarely do we see indications of this drawn-out chelicera in the Araneidae (Fig. 251). Although the proximally truncate chelicerae are a good distinguishing character of the Araneidae, they are also found in Linyphiidae.

While nesticid and mimetid palpi can be derived from a *Meta*-like palpus, so can the very simple palpus of the large linyphiid *Pimoa*. If the complicated

palpi of various araneoid families can be derived from a *Meta* and *Leucauge*-like palpus, might the ancestors of other araneoid families perhaps have made orb-webs, and might not the orb perhaps be the primitive web, the linyphiid and theridiid web specialized? The other as yet unsolved question is the relationship between the Araneoidea and the uloborids, which, like tetragnathids (but not other Araneoidea), also have trichobothria on the fourth femur and rest with the first two femora stretched forward.

METHODS OF STUDY

Examination Dish. To avoid unnecessary transfers of spider parts from a dish containing sand or from a dish with depressions in black paraffin (the first has disturbing reflections, the second insufficient light to see outlines), a new dish was made. A stender dish (inside diameter 50 mm, height 17 mm) with a ground glass cover was partly filled on one side with white paraffin available from grocery stores and on the other side with black paraffin, available from biological supply houses. To start, black paraffin was poured into the dish temporarily divided by cardboard. After a few minutes of cooling, the white was poured in on the other side and the cardboard removed. While still soft, various size depressions were made into paraffin to support spiders.

Measurements. Total length measurements of *Pachygnatha* were made, without the chelicerae, measuring from clypeus to posterior tip of the abdomen. About 10 specimens of each sex from different localities were measured to obtain total length. While going through the available collections, measurements of noticeably larger and smaller specimens were also recorded. Often, smaller and larger specimens were found throughout the range of the species. If there were geographic size differences, these were noted.

Genitalia. The female genital area of *Pachygnatha* was cut off, the tissue around the genital structure removed with sharpened needles, and the exposed genitalia submerged in clove oil for clearing and examination. Examination was done optimally when only partly cleared. After the clove oil was removed by washing in alcohol, the genital area was mounted from alcohol on a microscope slide into Hoyer's medium and examined in a Leitz-made Smith interference microscope.

Eyes. The eyes were examined in reflected light for tapetum, then cut off. The tissue behind was carefully teased away while placed above a light background, until the pigment outlining the rhabdoms became visible. This was done under a dissecting microscope. The illustrations are diagrammatic and composite, showing the tapetum in reflected light, the rows of rhabdoms in transmitted light. The left posterior median eyes are illustrated looking down vertically into the eye. The right posterior median is illustrated at its normal angle to the left eye (Fig. 300). The left lateral eyes are illustrated looking vertically into the eyes, as if both were facing the same direction.

Neotypes of Names. Article 75 of the International Code of Zoological Nomenclature (1961) restricts the use of neotype designation "only in connection with revisions in exceptional circumstances when a neotype is necessary in the interest of stability of nomenclature." Because of the confusion in the application of names in the genus *Pachygnatha*, neotypes were designated for two species in accordance with qualifying conditions of Article 75.

Tracheae. The tracheae of *Pachygnatha* and *Glenognatha* were examined by mounting the spiders on a microscope slide after most internal organs were teased away (some with venter, some with dorsum facing up). They were not boiled in sodium hydroxide since these tracheae are only lightly sclerotized.

Araneinae Latreille, 1806
Mecynogea Simon

Hentzia McCook, 1894, American Spiders, 3: 244. Type species by monotypy *Epeira basilica* McCook. Name preoccupied by *Hentzia* Marx, 1883.

Mecynogea Simon, 1903, Ann. Soc. Entom. Belgique, 47: 25. Type species designated by Petrunkevitch, 1928, Trans. Connecticut Acad. Sci., 29: 135, *M. bigibba* Simon, 1903, from Brazil. The name is feminine.

Allepeira Banks, 1932, Publ. Oklahoma Biol. Surv., 4: 23. New name to replace *Hentzia* McCook, preoccupied.

Diagnosis. *Mecynogea* differs from the related tropical *Cyrtophora* in the closely grouped eyes (Figs. 5, 8), in the more slender legs (Figs. 5, 7, 12) and in the shape of the abdomen whose sides are always more or less parallel (Figs. 5, 6). *Mecynogea* differs from most other araneid genera in the close spacing of the eyes, in the elongated abdomen, and in the slender, almost linyphiid-like legs with macrosetae. It differs from *Leucauge* and *Mangora* in its lack of the long trichobothria.

Coloration. Carapace light in most species, with lateral black longitudinal bands on thorax and a median longitudinal black line (Fig. 5). Abdomen with white or silver bands and black marks on dorsum and sides (Fig. 5). Venter dark, usually with a pair of longitudinal white or silver bands which may be broken (Fig. 6).

Structure. Carapace highest in head region with a shallow, indistinct thoracic depression, very narrow in front (Fig. 5). Height of clypeus less than diameter of anterior median eyes (Fig. 8). Eyes subequal in size, anterior median eyes sometimes slightly larger than others, especially in males; anterior lateral eyes sometimes slightly smaller. Eyes closely grouped, anterior median eyes their diameter apart, less than their diameter from laterals (Figs. 5, 8). Posterior median eyes their diameter or slightly more apart, the same distance from laterals. Posterior median eyes with characteristic narrow canoe tapetum and loops of rhabdoms as in species related to *Araneus* (Fig. 11). Chelicerae strong, endites almost as wide as long (Fig. 6). Legs slender, with long macrosetae, but no long trichobothria (Figs. 5, 7, 12). First leg longest, third shortest, second and fourth subequal in length, second leg of male being slightly longer than fourth. Abdomen almost three times as long as wide, sometimes with anteriodorsal humps, and with rounded posterior overhanging spinnerets (Figs. 5–7), widest anterior of middle (Fig. 5), at a slight angle to prosoma (Fig. 7). Males only slightly smaller than females. No leg articles modified (Fig. 12).

Genitalia. Female epigynum always has a projecting hood with a depression posteriorly containing the openings (Figs. 1–4). There is no scape. The seminal receptacles appear to be two dumbbell-like structures grown together (Fig. 3).

Femur of male palpus without proximal tooth (present in most Araneinae), and the endite lacks the facing tooth. Palpal patella with only one macroseta (Figs. 12, 14). The palpal structures (Fig. 15) are difficult to homologize with those of other araneids; they appear close to those of *Cyrtophora* and *Leucauge.* The homologies of Exline (1948) are almost certainly in error. *Mecynogea lemniscata* has a conductor (C in Fig. 15) and, unlike *Cyrtophora* species examined, there is no median apophysis. The filamentous embolus (E) is held by a structure which is probably not a terminal apophysis as thought by Exline (1948). This embolus is surprisingly similar to that of *Leucauge venusta.* Separated above the tegulum (T) at the base of the part which forms the embolus is a sclerotized loop, perhaps the radix. The filiform embolus of *Cyrtophora moluccensis* is also supported over part of its length by a basal outgrowth, and the palpus also has a sclerotized plate which is the radix. There is another lobe of uncertain homology above the embolus (Fig. 15).

Species. All species examined are very similar, but differ in structure of the

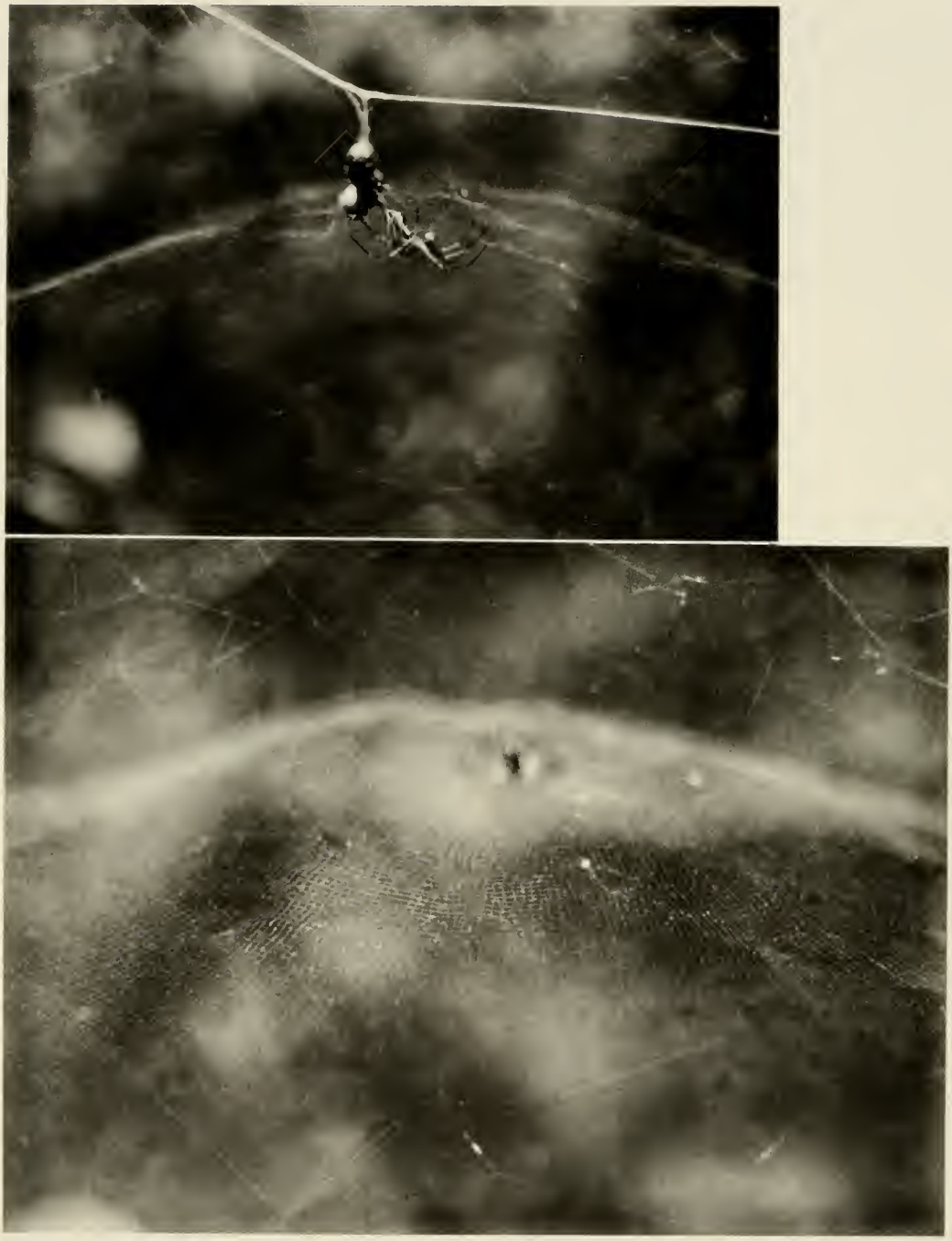
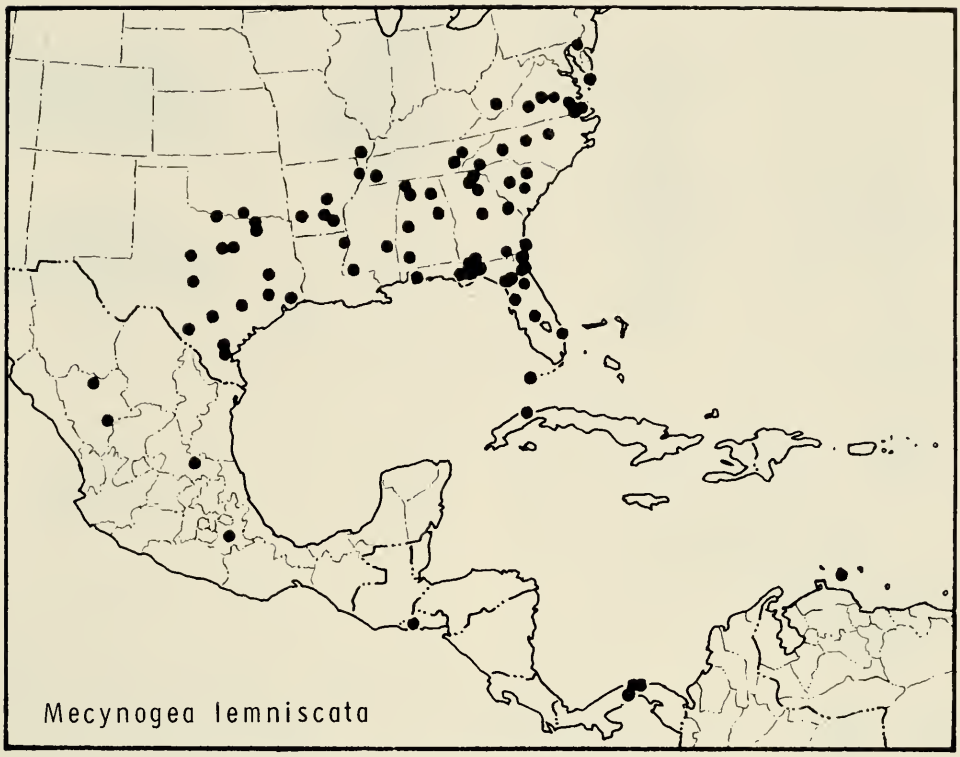


Plate 1. *Mecynogea lemniscata* (Walckenaer), above, female under web with three egg-sacs above; below, detail of web showing very small mesh. Web with dew.



Map 1. Distribution of *Mecynogea lemniscata* (Walckenaer).

genitalia and in the shape of the egg-sac. There may be half a dozen to a dozen species, all American, described in various genera. Most species are tropical or south temperate.

Natural History. *Mecynogea* makes webs like *Cyrtophora* (Plate 1) but no *Mecynogea* species are known to be colonial. The web is a small-mesh horizontal dome, lacking sticky silk. It has a barrier web above and below (Plate 1 and Exline, 1948).

Relationship. The canoe tapetum in the posterior median eyes and the looping rows of rhabdoms (Fig. 11) place *Mecynogea* in the Araneinae. Only *Cyrtophora* has a similar web, and the genitalia of *Cyrtophora* and *Mecynogea* can be derived from a common ancestor. The two genera are not close to each other however, although there is one species [*M. guianensis* (Keyserling)] (=*Cyrtophora grammica* Simon) which has intermediate genitalia. *Mecynogea* is not close to *Araneus* and other Araneinae. The palpal parts can at present not be readily homologized with those of palpi of the *Araneus* group. There is a resemblance of *Mecynogea* with *Mangora*: the shape of the abdomen and its angle to the prosoma, the many erect macrosetae on the legs (Fig. 7) and the narrow head. Whether this is superficial or an indication of relationship is not presently known. We will know more about the relationship after the tropical American *Cyrtophora* and *Mangora* have been studied.

Mecynogea lemniscata (Walckenaer)
Plate 1; Figures 1–15; Map 1

Linyphia lemniscata Walckenaer, 1841, Histoire Naturelle des Insectes Aptères, 2: 263. Name for illustration fig. 25, J. Abbot, 1792. Drawings of

the Insects of Georgia in America in the British Museum, Natural History. Photocopy at Museum of Comparative Zoology, examined.

Linyphia conferta Hentz, 1850, J. Boston Soc. Natur. Hist., 6: 30, pl. 4, fig. 7. Specimens from Alabama, destroyed.

Epeira basilica McCook, 1878, Proc. Acad. Natur. Sci., Philadelphia, p. 133, figs. 1–3, ♀. Specimens from Colorado River, southwest of Austin, Texas in the Academy of Natural Sciences, Philadelphia. One specimen from Texas marked *Epeira basilica* found and labeled by me as probable type.

Hentzia basilica:—McCook, 1893, American Spiders, 3: 244, pl. 14, fig. 2, pl. 23, fig. 8, ♀. Comstock, 1913, Spider Book, p. 417, fig. 430; 1940, rev. ed., p. 431, fig. 430. Bonnet, 1957, Bibliographia Araneorum, 2(3): 2157.

Cyrtophora basilica:—Simon, 1895, Histoire Naturelle des Araignées, 1(4): 771.

Allepeira basilica:—Banks, Newport and Bird, 1932, Publ. Univ. Oklahoma, Biol. Surv., 4: 23. Roewer, 1942, Katalog der Araneae, 2: 778.

Allepeira conferta:—Archer, 1940, Paper Alabama Mus. Natur. Hist., 14: 24.

Allepeira lemniscata:—Chamberlin and Ivie, 1944, Bull. Univ. Utah, Biol. Ser., 8(5): 93. Exline, 1948, Ann. Entomol. Soc. Amer., 41: 309, figs. 1–14, ♀, ♂, web, egg-sac.

Allepeira affinitata Kraus, 1955, Abhandl. Senckenberg. Naturforsch. Gesell., 493: 26, figs. 54–56, ♀, ♂. Male holotype from El Salvador in the Senckenberg Museum, Frankfurt, examined. NEW SYNONYMY.

Note. I follow here Exline (1948), who is the first revisor, in using Walckenaer's name *lemniscata*. The use of any other name for this species, although perhaps applied with more certainty, would not help the name stability. Abbot described the web of the spider, on the page facing the illustration, named by Walckenaer.

An old fashioned, unnecessarily detailed description of this species is found in Exline (1948).

Description. Living specimens. Legs, carapace, sternum greenish. Three longitudinal black bands on carapace (Fig. 5); sternum black on each side (Fig. 6). Femora with indistinct dark longitudinal lines. Median dorsal abdominal band laterally framed by a red line enclosing orange-yellow areas. Anterior of orange area a white patch; orange area divided by a median bluish black line and a transverse black mark; posteriorly orange area grades into median bluish black (Fig. 5). A white, wavy longitudinal line on each side of band; sides of abdomen bluish green (Fig. 7).

Female from northern Florida. Total length, 7.2 mm. Carapace, 2.7 mm long, 2.1 mm wide. First femur, 3.6 mm; patella and tibia, 3.8 mm; metatarsus, 3.2 mm; tarsus, 1.3 mm. Second patella and tibia, 3.0 mm; third, 2.0 mm; fourth, 3.2 mm.

Male from northern Florida. Total length, 5.5 mm. Carapace, 2.4 mm long, 1.8 mm wide. First femur, 3.7 mm; patella and tibia, 3.7 mm; metatarsus, 3.6 mm; tarsus, 1.3 mm. Second patella and tibia, 3.3 mm; third, 1.9 mm; fourth, 3.0 mm.

Variation. Female from 6.3 to 8.6 mm total length; carapace, 2.3 to 4.0 mm long, 1.6 to 2.9 mm wide; first patella and tibia, 3.3 to 5.4 mm long. Male from 4.0 to 6.6 mm total length; carapace 1.9 to 3.5 mm long, 1.4 to 2.4 mm wide; first patella and tibia, 3.2 to 5.5 mm long. The smallest specimens came from the northernmost localities, Delaware and Virginia; the largest from the Gulf Coast, Mexico to Panama and Cuba.

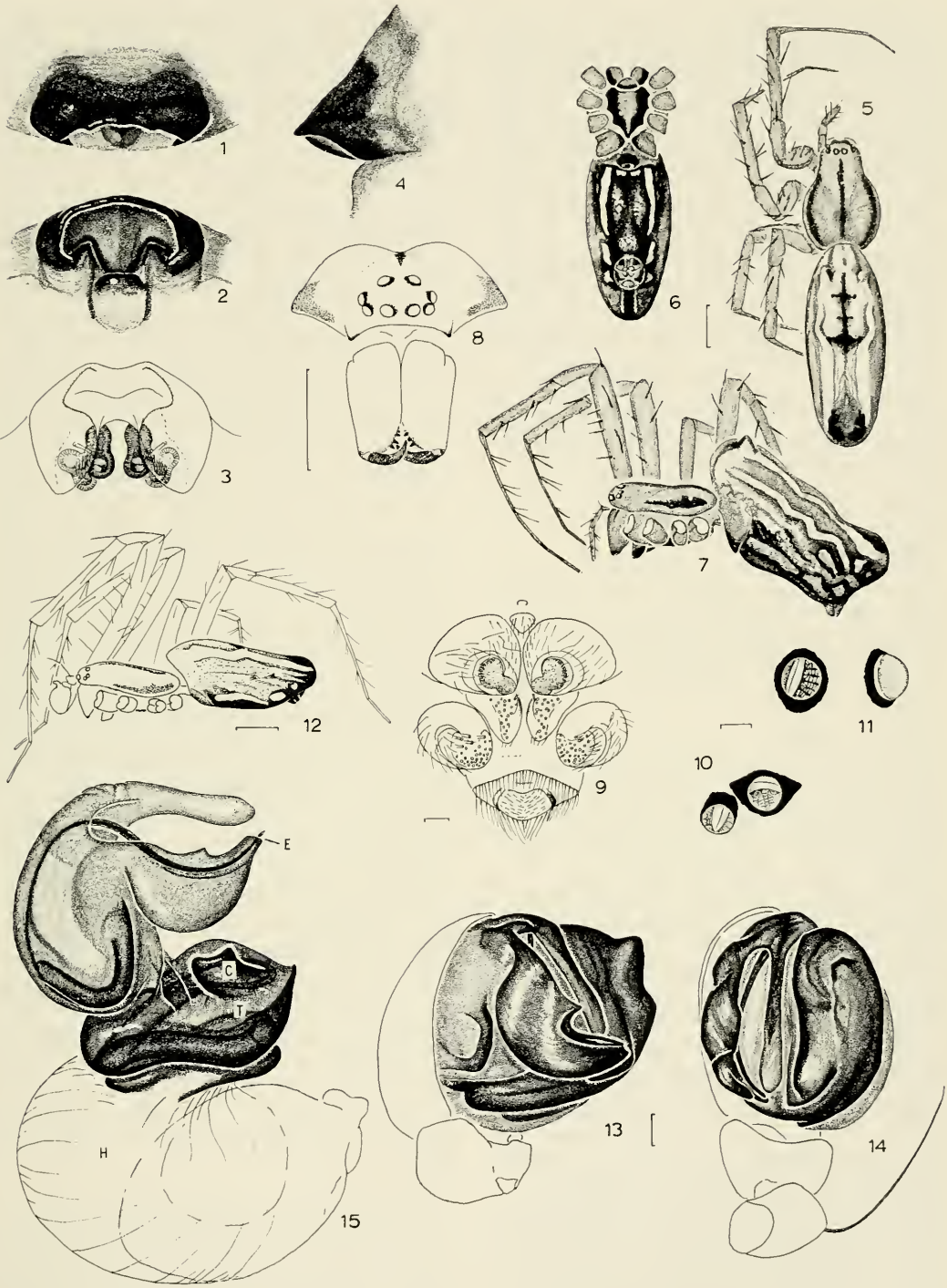
Diagnosis. Female. *Mecynogea lemniscata* lack bands on legs and have only some indistinct longitudinal lines on the femora; they differ from other species in the shape of the depression in the epigynum in posterior view (Figs. 2, 3); the male differs from other species in the shape of the sclerite, which holds the embolus filament and is visible in mesal view (Fig. 13).

→

Figures 1–15. *Mecynogea lemniscata* (Walckenaer). 1–11. Female. 1–4. Epigynum. 1. Ventral. 2. Posterior. 3. Posterior, cleared. 4. Lateral. 5. Dorsal. 6. Ventral. 7. Lateral. 8. Eye area and chelicerae. 9. Spinnerets. 10. Left lateral eyes. 11. Posterior median eyes. 12–15. Male. 12. Lateral. 13–15. Left palpus. 13. Mesal. 14. Ventral. 15. Mesal, expanded.

Scale lines. 0.1 mm; except Figures 5–8, 12, 1.0 mm.

Abbreviations. C, conductor; E, embolus; H, hematodocha; T, tegulum.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Natural History. The dome-shaped web is made in shrubs, usually in deciduous forest. Adult males are collected in various habitats in June and July. A Florida male was collected in January. Anderson (1978) reports that the spiderlings of egg-sacs produced "as early as June do not emerge until the end of March of the following year. The young are confined within the egg-sac for 290 days without access to food." There are records of spiders in urban areas. Many specimens in Texas were found as prey in mud-dauber wasp nests.

Distribution. Maryland to Missouri, Florida to Mexico and Panama, Cuba and Curaçao (Map 1). The northernmost locality is Chesapeake City, Maryland.

Metinae Simon, 1894
Misplaced species

Pseudometa biologica Chamberlin, 1925. Bull. Mus. Comp. Zool., 67: 217. Female holotype from Pacific Grove, Hopkins Laboratory, in the Museum of Comparative Zoology, examined, = *Zygiella x-notata* (Clerck). NEW SYNONYMY.

Nephila Leach

Nephila Leach, 1815, Zoological Miscellany; being Descriptions of New and Interesting Animals, London, 2: 133. Type species by monotypy *Nephila maculata* (Fabricius) from China. The name is feminine.

Diagnosis. Unlike most other araneid genera the labium of the female is longer than wide (Fig. 24). Both sexes of *Nephila* differ from the related *Leucauge* in the lack of femoral trichobothria. Female *Nephila* differ from *Nephilengys* in lacking strong setae on the head; also the carapace length is shorter than the fourth patella and tibia. The long filamentous embolus wrapped in the conductor and projecting at right angles from the palpal axis (Figs. 21, 22, 42, 43) is distinctive for *Nephila*, not present in *Nephilengys*. The first patella and tibia is about 1.4 times carapace length, in *Nephilengys* only 1.2. The first tarsus is about 1.7 times patella and tibia length, that of *Nephilengys* only 1.2.

Description. Female. Carapace very wide in front, with a transverse groove as a thoracic depression (Figs. 33, 36), sometimes with two horns in posterior head region anterior to the thoracic depression (Figs. 35, 36). An oval depression between head and thorax in cervical groove (Figs. 31, 36). Clypeus height about 1 to 2 diameters of anterior median eyes (Figs. 23, 34, 35). Eyes subequal in size, laterals slightly smaller than medians. Secondary eyes with canoe tapetum (without loops or rows of rhabdoms), as in *Meta* and most Araneoidea, other than Araneinae and Tetragnathinae* (Figs. 37, 38). Anterior median eyes 1.5 diameters apart, slightly more than 3 from laterals. Posterior median eyes more than 1.5 diameters apart, more than 3.5 from laterals. Laterals on a tubercle, anterior laterals separated by more than their diameter from posterior laterals (Figs. 33, 36). Chelicerae strong with about 3 teeth on anterior margin, 3 on posterior (Fig. 24) and a smaller tooth facing tip of fang. Group of setae covering face of anterior margin (Fig. 34). Endites and labium very long (Fig. 24). Metatarsi and tarsi of legs longer than patellae and tibiae (Fig. 31). First legs longest, second next in length, third shortest. Metatarsi often with setae resembling a bottle brush (Fig. 31). Leg tips have the sustentacular setae less visible than in other genera (Levi, 1978b), but they are present. Abdomen elongate, cylindrical, longer than wide (Figs. 19, 20, 31, 32, 41).

Male. Smaller than female, total length less than half total length of female (Fig. 41). Carapace with some shallow depression between head and thorax and very shallow thoracic depression (Fig. 41). Height of clypeus is slightly less than di-

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* *Nephila maculata* has secondary eyes with canoe-shaped tapetum, but the reflecting pigment crystals are reduced. The main eyes are large with many rhabdoms, the secondary eyes small with few. The eyes are not like those of *Araneus*, but like those of *Meta* (Homann, by correspondence, October, 1979).

ameter of anterior median eyes. Anterior median eyes slightly the largest, less than their diameter apart, the same distance from laterals. Posterior median eyes their diameter apart, 1.6 diameters from laterals. Anterior and posterior lateral eyes touching. There are no leg modifications; the trochanters may appear notched. In several species studied, the males come in various size classes (Gerhardt, 1929).

Genitalia. The epigynum consists of a transverse fold (Figs. 16–18, 28–30) and a groove in posterior view with the opening on each side ventral in the groove (Figs. 18, 30). The seminal receptacles are heavily sclerotized (Figs. 16, 28) and there is a fertilization duct.

The duct of the palpus is coiled within the almost spherical tegulum (Figs. 22, 25, 43). The embolus filament is held and wrapped within the conductor (Figs. 25, 26).

Natural History. Nephila females make a large web with many radii, the hub located above center (Plate 2), and with the temporary spiral not removed. The web and behavior of *N. maculata* of New Guinea have been studied by Robinson and Robinson (1973, 1976).

Species. Perhaps 20 species of *Nephila* are found in the tropics of various parts of the world, only one in the Americas, *N. clavipes*. They have been revised by Dahl (1912), the African species by Benoit (1962, 1964). Unfortunately, both papers lack essential illustrations. The long paper by Dahl is of limited use and is out-of-date (freely translated, p. 80):

> "In order to facilitate species recognition by the amateur, I proceeded on the following principles: 1) the species are grouped by their occurrence in our [German] colonies; 2) I considered only large females, since smaller ones and males are overlooked; 3) I have only used color marks. I do not give figures since especially in spiders they may be misleading. Unimportant color and marks usually show up better in illustrations than those used for recognition of the species."

Relationship. Nephila is known to be close to *Nephilengys*. Although quite similar in structure, *Nephilengys* makes a more conservative orb-web, more like that of other Araneidae (M. Robinson, personal communication). *Leucauge*, judging by the unusual structure of the palpus, the base of the embolus located between tegulum and cymbium (Figs. 25, 26 and 58, 59), is also close to *Nephila*.

Nephila maculata Fabricius
Figures 16–22

Aranea maculata Fabricius, 1793, Entomologia Systematica, 2: 425. [Not *A. maculata*, Olivier, 1789 = *Steatoda albomaculata* (De Geer).]

A. pilipes Fabricius, 1793, Entomologia Systematica, 2: 425.

Nephila maculata:—Leach, 1815, Zool. Misc., 2: 134, pl. 110. Dahl, 1912, Mitt. Zool. Mus., Berlin, 6: 35, 52. Bonnet, 1958, Bibliographia Araneorum, 2: 3074.

Nephila pilipes:—Roewer, 1942, Katalog der Araneae, 1: 929.

Note. Despite the original homonymy of the name, the specific name *maculata* has been used in almost all literature except Roewer.

The type species of the genus is found from China and India to the southwestern Pacific Islands. It is common in New Guinea and the Philippines.

Nephila clavipes (Linnaeus)
Plate 2; Figures 23–43; Map 2

Aranea clavipes Linnaeus, 1767, Systema Naturae, 12th ed., p. 1034. Name given to specimens from Jamaica illustrated by Patrik Browne, 1756, *The Civil and Natural History of Jamaica*, London, p. 419, pl. 44, fig. 4.

Aranea longimana Fabricius, 1781, Species Insectorum, Hamburg et Kilonii, 1. Aran. p. 536. Specimens from Cayenne.

Nephila plumipes:—C. L. Koch, 1839, *Die Arachniden*, 6: 138, pl. 529. Not *N. plumipes* (Latreille).

Nephila wilderi McCook, 1893, American Spiders, 3: 251, pl. 7, figs. 1, 2, pl. 23, figs. 6, 7, ♀, ♂. Syntypes from southern Atlantic and Gulf coasts to southern California and West Indies, lost. [The California specimens probably belonged to the Marx collection.]

Nephila wistariana McCook, 1893, American Spiders, 3: 252, pl. 23, figs. 2, 3, ♀, ♂. Syntypes from Caribbean Sea, Louisiana and Texas, lost.

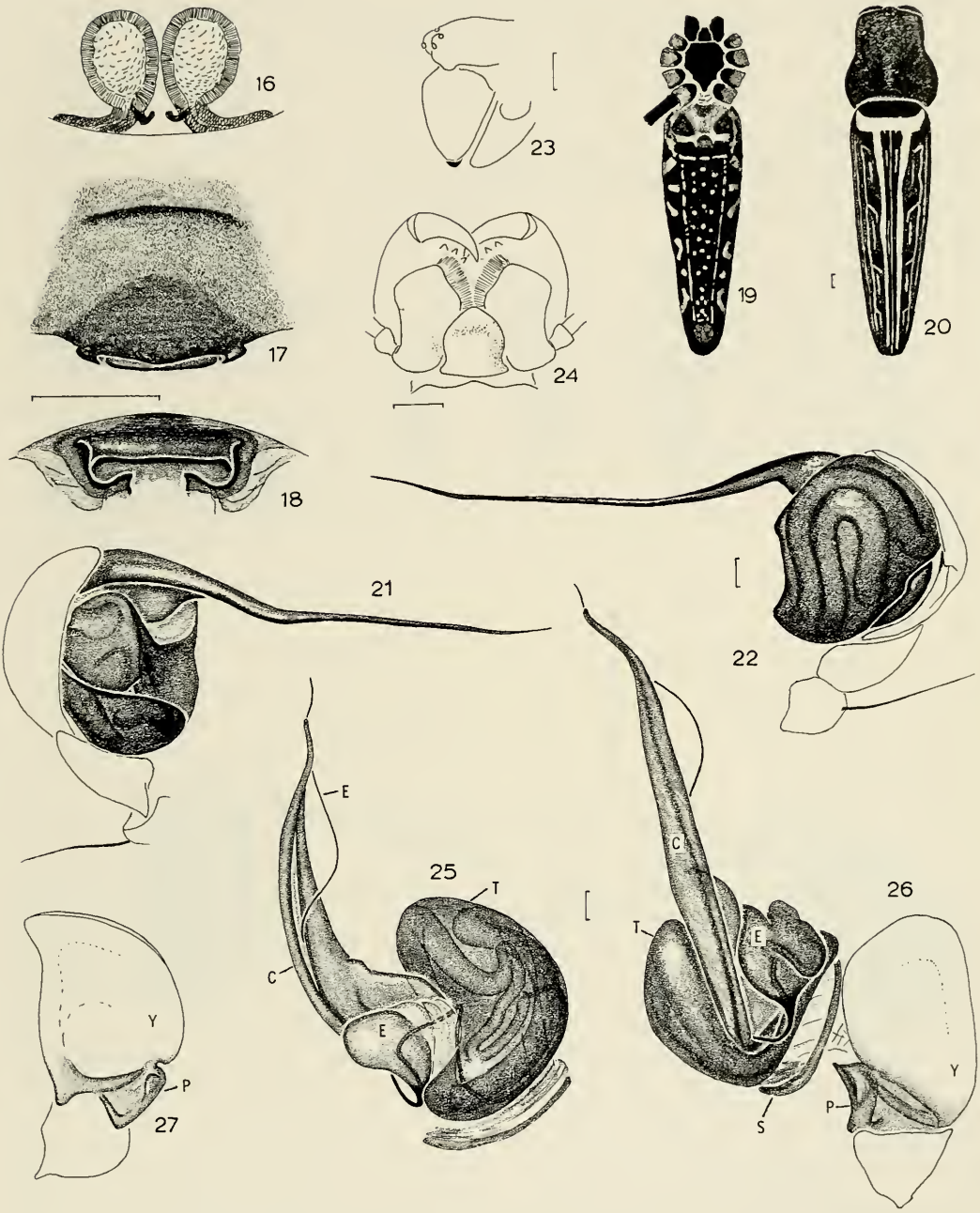
Nephila concolor McCook, 1893, American Spiders, 3: 256, pl. 23, fig. 1, ♀. Female from southern California, erroneous G. Marx locality, lost.

Nephila clavipes:—McCook, 1893, American Spiders, 3: 255, pl. 24, fig. 1, ♀. F. P.-Cambridge, 1901, Ann. Mag. Natur. Hist. (ser. 7), 7: 325, pl. 7, figs. 1–4, ♀, ♂; 1904, Biologia Centrali-Amer-

Plate 2. *Nephila clavipes* (Linn.) web. Web dusted with cornstarch.

icana, Araneidea, 2: 448, pl. 42, figs. 23, 24, ♀. Dahl, 1912, Mitt. Zool. Mus. Berlin, 6(1): 46, 73, 75, ♀. Comstock, 1912, *The Spider Book*, p. 426, figs. 437–441, ♀, ♂, web. Petrunkevitch, 1930, Trans. Connecticut Acad. Sci., 30: 247, figs. 101, 102, ♀, ♂. Comstock, 1940, *The Spider Book*, p. 440, figs. 437–441, ♀, ♂, web. Roewer, 1942, Katalog der Araneae, 1: 932. Bonnet, 1958, Bibliographia Araneorum, 2: 3068. Archer, 1958, Amer. Mus. Novitates, no. 1958: 2, figs. 1, 2, ♀, ♂. Wiehle, 1967, Senckenbergia Biol., 48: 194, fig. 49, ♀.

Nephila thomensis Benoit, 1963, Entom. Mitt., Zool. Staatsinst. Zool. Mus. Hamburg, 2(41): 5, figs. 1–3, ♀. Female holotype and paratypes from São Tomé, Africa, 28.III.1898, in the Zoologisches Staatsinstitut und Zoologisches Museum, Hamburg, paratype examined. NEW SYNONYMY.

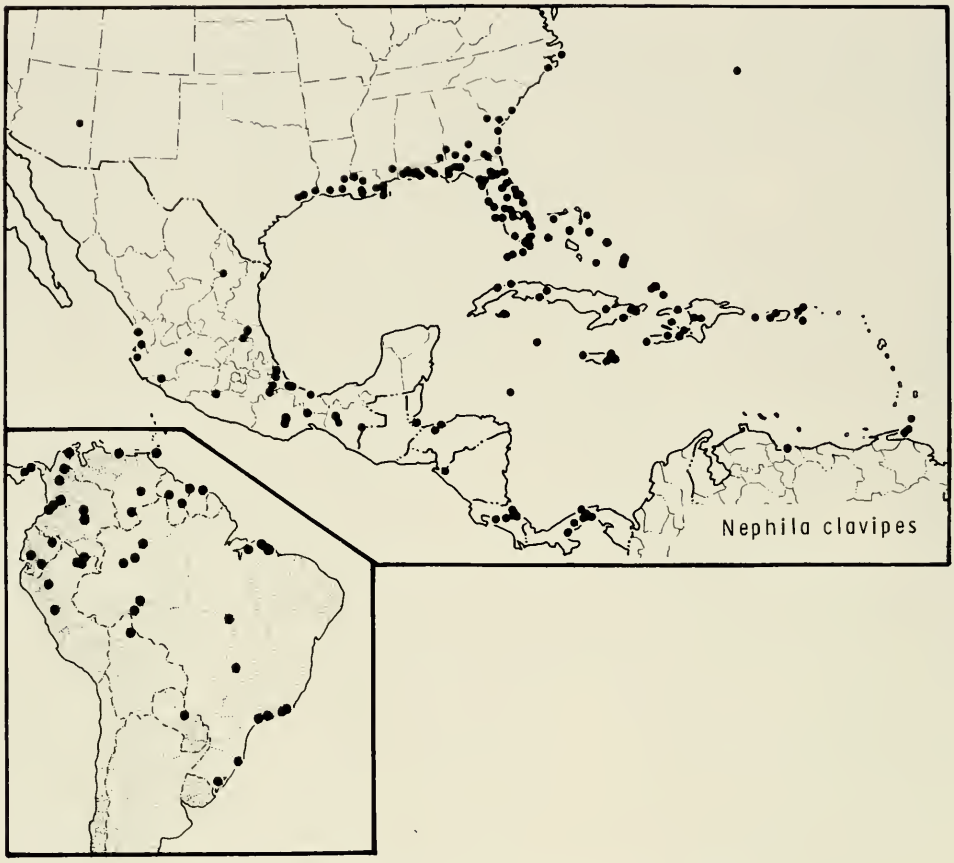


Figures 16–22. *Nephila maculata* (Fabricius) female from Philippines, male from Java. 16–20. Female. 16–18. Epigynum. 16. Dorsal, cleared. 17. Ventral. 18. Posterior. 19. Ventral, legs removed. 20. Dorsal, legs removed. 21, 22. Left male palpus. 21. Mesal. 22. Lateral.

Figures 23–27. *N. clavipes* (Linnaeus). 23, 24. Female. 23. Head and chelicera. 24. Labium and endites. 25–27. Left palpus expanded. 25. Submesal. 26. Dorsal. 27. Cymbium, ventral.

Scale lines. 1.0 mm; Figures 21–22, 25–27, 0.1 mm.

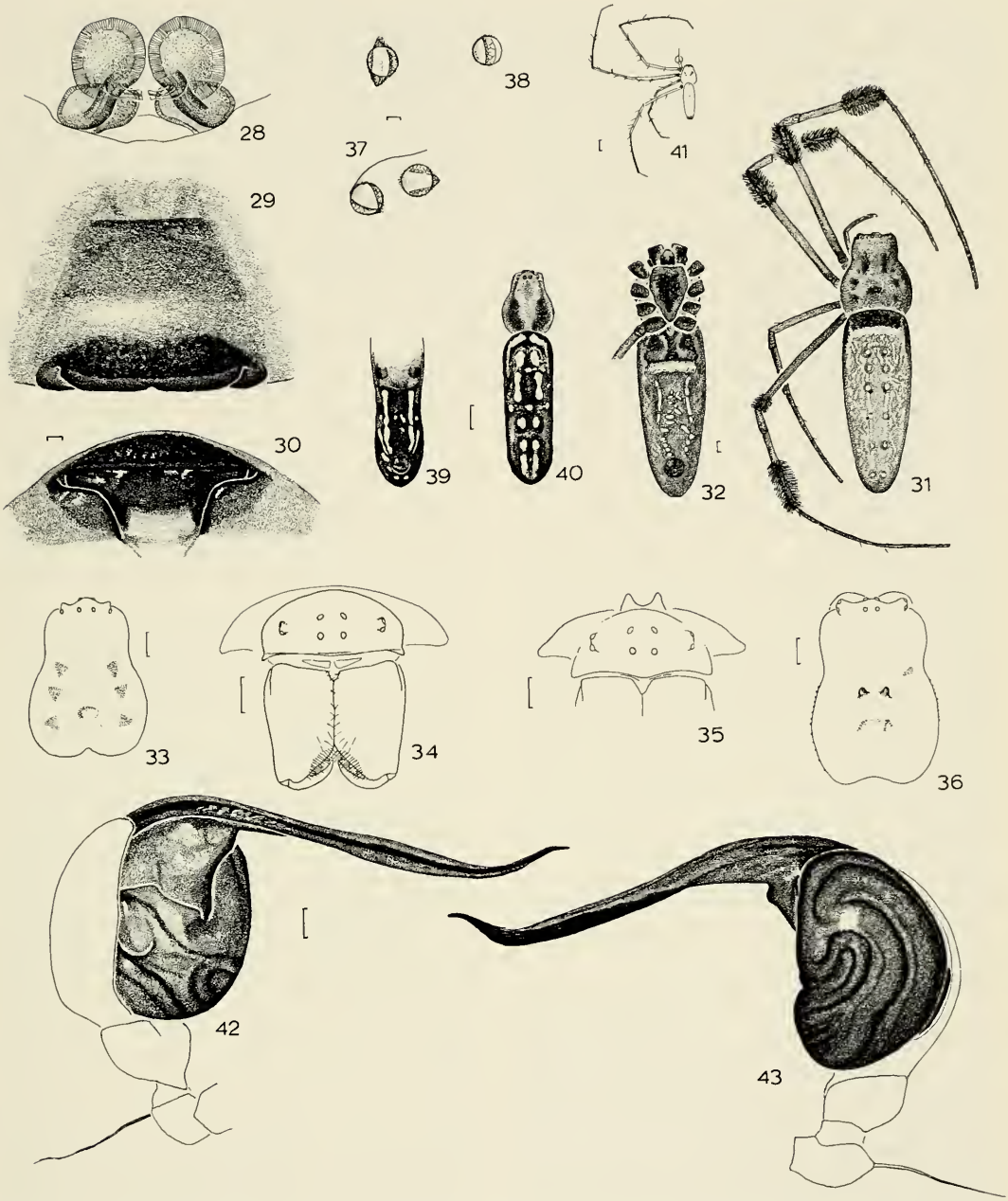
Abbreviations. C, conductor; E, embolus; T, tegulum; P, paracymbium; S, subtegulum; Y, cymbium.



Map 2. American distribution of *Nephila clavipes* (Linnaeus).

Description. Female from Florida. Carapace yellow-brown covered by white setae; three pairs of dark brown patches; thoracic groove also dark (Fig. 31). Chelicerae, endites, labium dark brown with distal edge of labium and endites light; sternum orange, darker in middle (Fig. 32). Coxae ventrally yellow-brown, dark brown anterior and posterior. Legs yellow; setae black (Fig. 31). Dorsum of abdomen with a dark transverse patch anteriorly, a light transverse mark behind, and pairs of light spots posteriorly (Fig. 31). On venter two parallel longitudinal light lines with intervening irregular white marks (bordered by dark) (Fig. 32). Indistinct white marks in a marbelized pattern on sides. Living specimens are greenish. Legs with tufts of hair on distal ends of femur and tibia of legs 1, 2 and 4, but not always present (Fig. 31). Abdomen overhangs spinnerets slightly (Fig. 32). Total length, 23.0 mm. Carapace, 8.4 mm long, 5.4 mm wide. First femur, 14.2 mm; patella and tibia, 14.4 mm; metatarsus, 18.0 mm; tarsus, 3.6 mm. Second patella and tibia, 11.4 mm; third, 5.8 mm; fourth, 11.0 mm.

Male. Carapace orange-yellow. Dark marks on each side of head in depression (Fig. 41). Chelicerae orange-yellow. Sternum orange with white pigment in center, some dark opposite each coxa. Legs orange-yellow. Dorsum of abdomen has a shiny, dark cardiac mark and scattered small white pigment spots in two longitudinal bands on each side (quite variable). Posterior tip of abdomen dark as in



Figures 28–43. *Nephila clavipes* (Linnaeus). 28–38. Female. 28–30. Epigynum. 28. Dorsal, cleared. 29. Ventral. 30. Posterior. 31. Dorsal. 32. Ventral. 33–36. Carapace. 34, 35. Head and chelicerae. 33, 34. (Florida). 35, 36. (Iquitos, Peru). 37. Left lateral eyes. 38. Posterior median eyes. 39, 40. Juvenile. 39. Ventral. 40. Dorsal. 41–43. Male. 41. Dorsal. 42, 43. Left male palpus. 42. Mesal. 43. Lateral.

Scale lines. 1.0 mm; Figures 37, 38, 42, 43, 0.1 mm.

Leucauge. Sides with white dots on orange. Venter gray in center and on each side of longitudinal white lines. White lines in turn made up of white pigment dots on orange. Total length, 5.8 mm. Carapace, 2.4 mm long, 1.7 mm wide. First femur, 5.3 mm; patella and tibia, 5.0 mm; metatarsus, 6.8 mm; tarsus, 2.2 mm. Second patella and tibia, 4.2 mm; third, 1.9 mm; fourth, 3.3 mm.

Variation. In South American specimens the leg brushes are less distinct. Most surprising are the two horns (Figs. 35, 36) present on the carapace of females from the Amazon Basin; females from Rio de Janeiro and southwestern Ecuador, Trinidad and Peru have small horns.

Archer called "the tufted race [with strong leg-brushes] which occurs in Jamaica, other parts of the Caribbean region, North America, Middle America and South America *N. c. fasciculata* (De Geer)," restricting *N. c. clavipes* to Cuba and Hispaniola. This was done despite the fact that Linneaus named a Jamaican spider *clavipes*. Specimens with horns were placed by Archer in *Nephila cornuta* (Pallas) and into Archer's new subgenus *Nothonephila*. Archer ascribes F. P.-Cambridge's observation of specimens with small horns to juveniles. However, Archer's observations are in error and F. P.-Cambridge and Dahl are correct in saying there are adult intermediates with small horns.

In posterior view the median piece of the epigynum in most specimens other than those from Florida is wider than the one illustrated (Fig. 30). The dorsum of the abdomen may be slightly sclerotized in larger males (Fig. 41). The sizes of individuals differ enormously, a variation which does not appear to be geographic. Females measured 19 to 34 mm total length; carapace, 6.8 to 12.1 mm long, 4.9 to 8.6 mm wide; first patella and tibia, 12.5 to 19.4 mm. Southeastern males measured 4.6 to 10.5 mm total length; carapace, 1.8 to 4.5 mm long, 1.5 to 3.1 mm wide; first patella and tibia, 3.4 to 10.3 mm. A male from British Guiana was 2.6 mm total length; carapace, 1.4 mm long, 1.1 mm wide.

Diagnosis. As far as is known this is the only species of *Nephila* in the Americas. Females can readily be separated from other American orb-weavers and species of *Nephila* from other parts of the world by the abdomen coloration, the dorsum having an anterior black transverse bar, followed by both a white bar which fades out on the sides posteriorly and by the two irregular rows of spots (Fig. 31). The venter also has a white bar posterior to the epigynum (Fig. 32). The epigynum has cornicular sculpturing on the ventral median portion, while the posterior part is smooth, with the opening on each side (Figs. 29, 30). The male *Nephila* can readily be recognized by the long conductor of the palpus which encloses the embolus. The shape of the tegulum, the convolutions of the duct inside, and the long conductor with a twist near the tip (Figs. 42, 43) are diagnostic for the species.

Natural History. *Nephila clavipes* occurs only in the warmer parts of the southeastern United States in mesic to moist deciduous hardwoods and swamps. In Simberloff's studies of recolonization of islands whose fauna was destroyed, *Nephila clavipes* was the first orb-weaver and among the first spiders to appear (Simberloff and Wilson, 1970; Simberloff, 1976). Adult males have been collected from May to September in the southeastern states; one male from Orange County, Florida was collected in December. But males are found in February and March in the West Indies. Adult females can be found all year. The web has been described and illustrated by Comstock (1912, 1940). It is found at 1 to 6 m heights. It is 60–90 cm in diameter, the hub near the top, and contains many radii (Plate 2). The temporary spiral is not removed and a barrier web may be next to it. Only parts of the viscid spiral are replaced at a time; it is not remade daily like that of most orb-weavers. The silk is yellow. The important behav-

ior studies are those of Robinson and Mirick, 1971, Robinson and Robinson, 1974, and Christenson and Goist, 1979.

Distribution. Southeastern United States to northern Argentina (Map 2). There are several records from California, but all are from the Marx Collection, whose locality data is often in error. There are no recent finds from California. The most northwestern record is Showlow, Arizona, 28 August 1965, ♀ (F. Matzone); the most northern, Orracoke, Blackbeards Hammock, Hyde County, North Carolina, 25 August 1976, several females, males (J. Coddington) and a sight record "common near the coast in Beaufort, North Carolina in 1966," and "in 1976 when I visited Beaufort . . . the same places were occupied by *Argiope*" (P. Weygoldt, in letter). Another interesting record is São Tomé Island, off Gabon, Africa.

Leucauge White 1841

Leucauge White, 1841, Ann. Mag. Natur. Hist., 1(7): 473. Type species by monotypy *Linyphia* (*Leucauge*) *argyrobapta* White from near Rio de Janeiro. The name was first proposed as a subgenus. The name is feminine.

Argyroepeira Emerton, 1884, Trans. Connecticut Acad. Sci., 6: 331. Type species by monotypy *Epeira hortorum* Hentz (=*Leucauge venusta*).

Opas O. P.-Cambridge, 1889, Biologia Centrali-Americana, Araneidea, 1: 184. Type species designated by F. P.-Cambridge, 1903, *O. lugens*.

Plesiometa F. P.-Cambridge, 1903, Biologia Centrali-Americana, Araneidea, 2: 438. Type species by monotypy and by original designation *P. argyra*.

Note. The specimens of *L. argyrobapta* (White) are lost. The identity of the species is not known.

Diagnosis. Leucauge differs from *Nephila* in the presence of long, feathered trichobothria, proximally and on the anterior surface of the femur of the fourth leg (Figs. 50, 51, 67). Also the labium of *Leucauge* is wider than or as wide as long, rather than longer than wide (Fig. 53). Close to *Leucauge* are two genera, *Alcimosphenus* (with two species in the West Indies) and the neotropical *Mecynometa*. Both also have the rows of trichobothria on the fourth femur. *Alcimosphenus* has more colored pigment and is darker. *Mecynometa* is silver and black, the abdomen having a tail that extends beyond the spinnerets, and the fourth coxae spaced farther apart. It is possible that these two genera cannot be kept separate from *Leucauge*.

Description. Carapace relatively wide in front, with a deep transverse thoracic depression, deeper on each side (Fig. 50). A round or oval diagonal depression between head and thorax in the cervical groove on each side (Fig. 50) (also present in *Nephila*). Eyes subequal in size. Anterior median eyes about their diameter apart, one to two diameters from laterals. Posterior median eyes about one diameter apart, 1.5 to 2 diameters from laterals. Secondary eyes with canoe tapetum (Figs. 48, 49, 65, 66). Clypeus height equals diameter of the anterior median eye (Figs. 47, 54, 64). Sternum has some setae, longest setae anteriorly. Chelicerae strong with about three pairs of teeth on the anterior, three or four on the posterior margin (Figs. 47, 53, 64). Endites of the palpal coxae are longer than wide and wider distally than proximally (Fig. 53). Legs are fairly long, the first longest, second next, third shortest. Abdomen longer than wide, sides subparallel with characteristic silver coloration, broken in several longitudinal lines (Fig. 50). Short trichobothria are found on tibiae and base of femora, none on metatarsi.

Male. Only slightly smaller than female, with longer legs. Median eyes slightly larger than laterals, and eyes grouped closer together. Clypeus height equals radius of anterior median eyes. Chelicerae weaker than female, with two anterior teeth, two to four posterior. Except for increased length, no other leg modifications. Color is like that of the female.

Genitalia. Epigynum with two ventral lateral openings leading into sclerotized and variable pockets (difficult to discern) (Figs. 45, 46). Fertilization ducts

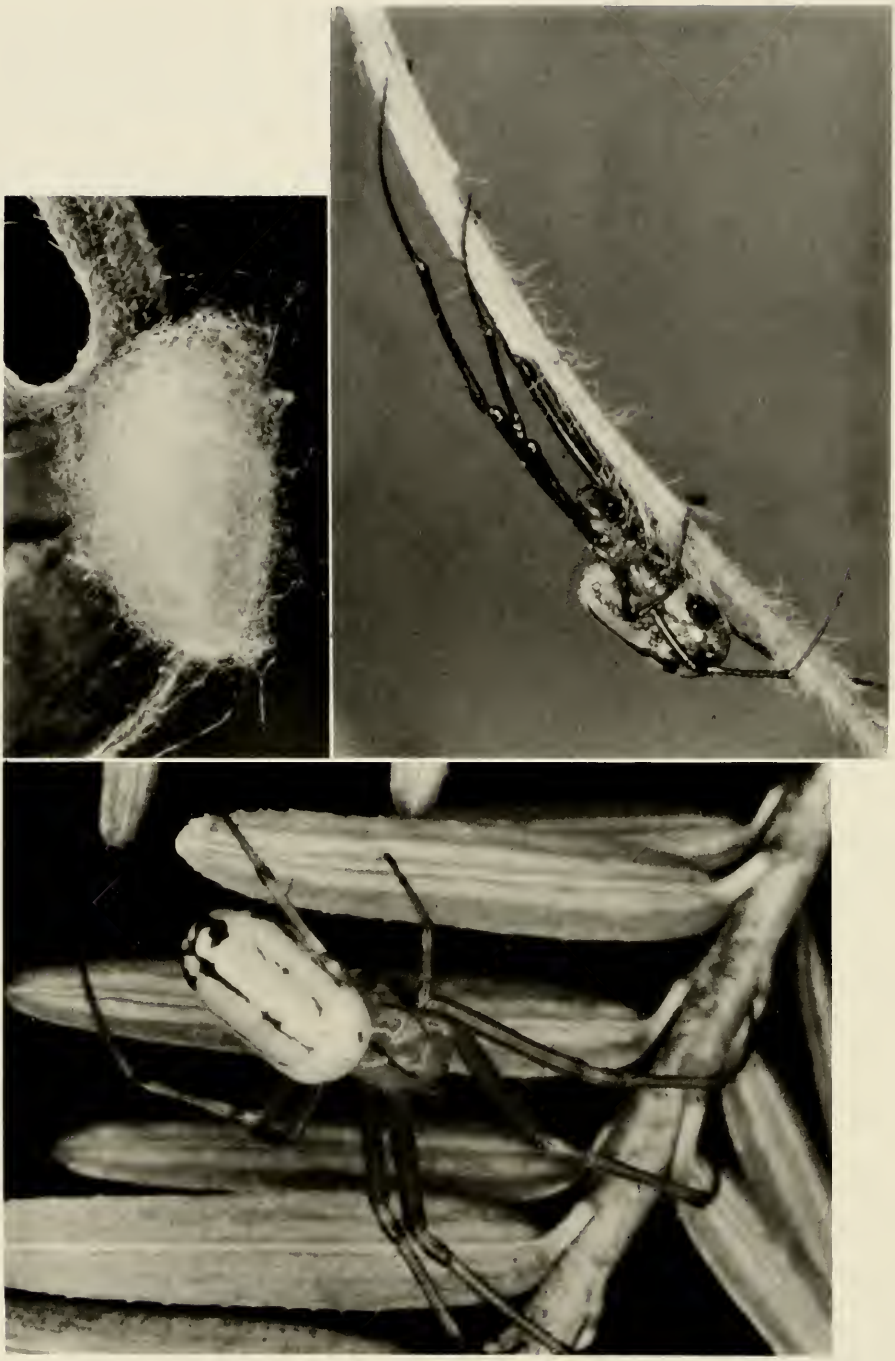


Plate 3. *Leucauge venusta* (Walckenaer), female. Upper left egg-sac, with inner silk orange colored; diameter 7 mm. Upper right, specimen from Florida; below, specimen from Massachusetts.

present (Fig. 44). Seminal receptacles unusually thin-walled (Figs. 44, 60) and sometimes appear partly digested in alcoholic collections. Thin-walled receptacles are also found in *Azilia*; the significance of the similarity is not known.

Palpus very simple with a large spherical tegulum containing coiled duct (Figs. 56–59, 70). Embolus with an ovate base and a thread-like tip held by a conductor; conductor coiled around thread (Figs. 58, 59, 69, 71).

Species. *Leucauge* species are mainly tropical, world-wide. They differ only slightly in coloration and in proportions of the epigynum; and in the shape of the male bulb and conductor of the palpus.

Natural History. *Leucauge* makes large orbs, most horizontal, with many radii and large numbers of sticky threads (Plate 4). Some species are colonial.

Relationship. *Leucauge* has at various times been placed with *Tetragnatha*. Palmgren (1979) suggests using some internal characters to show relationship with *Tetragnatha*. The short trichobothria at the base of the femora are also like those of *Tetragnatha*. However, other characteristics indicate that *Leucauge* is more closely related to other genera. The eye structure indicates the genus is close to *Meta*; *Leucauge* is obviously a close relative of *Nephila*. The structure of the palpus of *Nephila* and *Leucauge* is very similar: the base of the embolus hidden between cymbium and bulb is an unusual specialization found in both genera. The long endites are characteristic of both genera, the pair of depressions between head and thorax characteristic of both. Male *Nephila* have the abdomen shaped like that of *Leucauge* and also have a darker posterior end. A third genus belonging to this group is *Nephilengys*. *Nephila* and *Nephilengys* differ by lacking *Leucauge*'s rows of trichobothria on the fourth femur and by having giant females and dwarf males.

Key to *Leucauge* Species North of Mexico

1. Females and juveniles 2
– Males 3

2(1). Epigynum with median depression (Fig. 45); middle of venter of abdomen with tiny silver specks and two triangular marks (Fig. 51); Ontario, eastern states to California (Map 3) ..... *venusta*
– Epigynum with a median cone (Figs. 61–63); venter of abdomen with two longitudinal silver lines, without silver specks in between (Fig. 67); Florida (Map 3) ..... *argyra*

3(1). Palpal tibia as long or longer than cymbium (Fig. 56); cymbium without dorsal hook (Fig. 57); Ontario eastern states to California (Map 3) ..... *venusta*
– Palpal tibia shorter than cymbium (Fig. 68); cymbium with a dorsal hook (Fig. 69); Florida (Map 3) ..... *argyra*

Leucauge venusta (Walckenaer)
Plates 3, 4; Figures 44–59; Map 3

Epeira venusta Walckenaer, 1841, Histoire Naturelle des Insectes Aptères, 2: 90. Name given to Abbot's illustration of Georgian Spiders, p. 13, fig. 113. Photocopy in the Museum of Comparative Zoology, examined.

Epeira hortorum Hentz, 1847, J. Boston Soc. Natur. Hist., 5: 477, pl. 31, fig. 19. Females from the United States, destroyed.

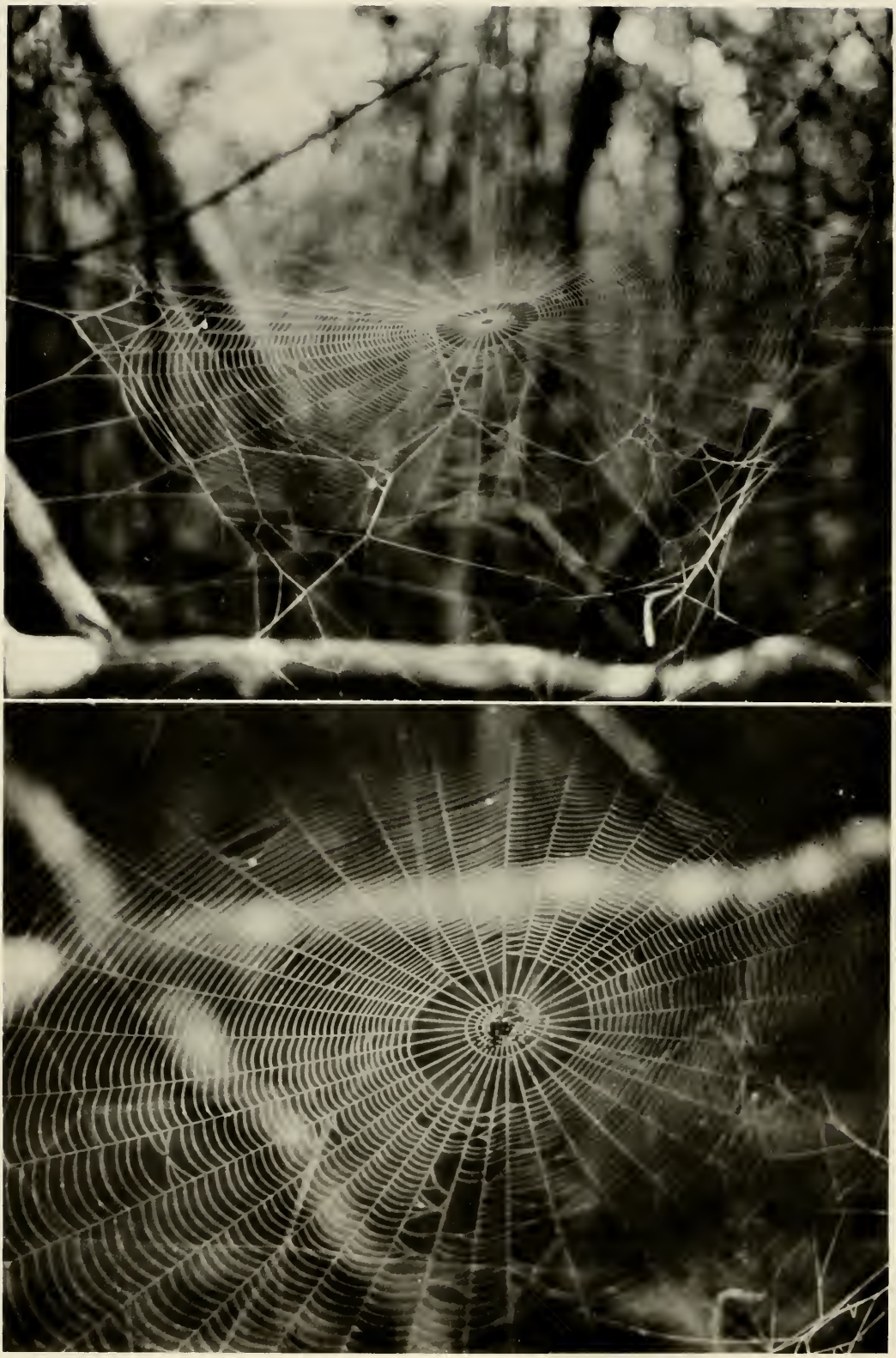
Argyroepeira hortorum:—Emerton, 1884, Trans. Connecticut Acad. Sci., 6: 332, pl. 37, figs. 29–32, ♀, ♂. Keyserling, 1893, Spinnen Amerikas, 4: 333, pl. 17, figs. 246. Emerton, 1902, Common Spiders, p. 192, figs. 446, 447, ♀.

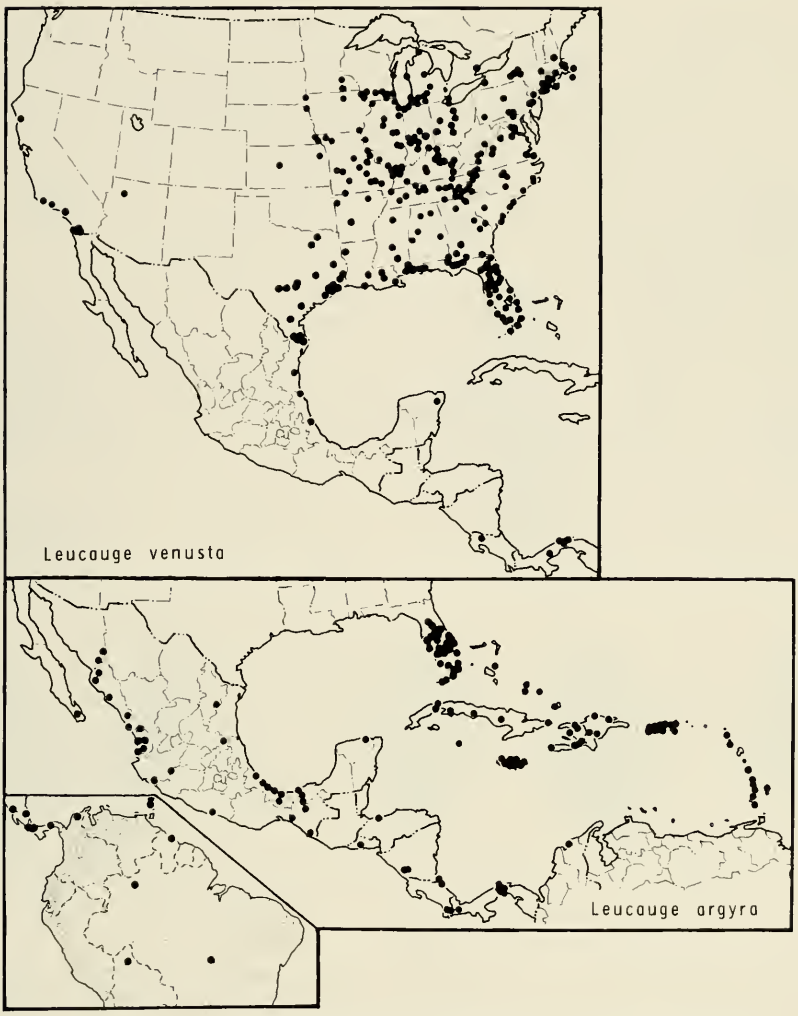
Argyroepeira venusta:—McCook, 1893, American Spiders, 3: 242, pl. 20, figs. 1–6, ♀, ♂.

Leucauge venusta:—F. P.-Cambridge, 1903, Biologia Centrali-Americana, Araneidea, 2: 441, pl. 42, figs. 1, 2, ♀, ♂. Comstock, 1912, *The Spider Book*, p. 422, figs. 429, 434–436; 1940, rev. ed., p. 436, figs. 429, 434–436, ♀, ♂, web. Roewer, 1942, Katalog der Araneae, 1: 1012. Kaston, 1947, Bull. Connecticut Geol. Nat. Hist. Surv., 70: 265, figs. 836–837, 843–846, ♀, ♂. Bonnet, 1957, Bibliographia Araneorum, 2: 2477.

Leucauge (*Argyroepeira*) *mabelae* Archer, 1951, Amer. Mus. Novitates, no. 1487: 6, figs. 1, 2, ♀, ♂. Male holotype from Sarasota, Sarasota County, Florida in the American Museum of Natural History, examined. NEW SYNONYMY.

Description. Female from Florida. Carapace, sternum, legs orange-brown when in alcohol, green in life. Labium and endites with some black pigment. Dorsum of abdomen silver, made of tiny coalescing spots; no spots in midline, and in branches from midline (Fig. 50). On sides posteriorly, living specimens have yellow pigment which gives a golden iridescent color. Some also have red pig-





Map 3. Distribution of *Leucauge venusta* (Walckenaer) and *L. argyra* (Walckenaer).

ment. Posterior of abdomen black. Venter with two silver triangles containing fused pigment spots, often red to orange in living specimens (Fig. 51). More scattered silver pigment outside the triangles, green and some black pigment in living specimens. Total length, 5.9 mm. Carapace, 2.2 mm long, 1.7 mm wide. First femur, 4.2 mm; patella and tibia, 4.8 mm; metatarsus, 3.8 mm; tarsus, 1.3 mm. Second patella and tibia, 3.7 mm; third, 1.5 mm; fourth, 2.9 mm.

Male from Florida. The abdomen narrows posteriorly, unlike that of the female. Total length, 5.2 mm; carapace, 2.0 mm long, 1.7 mm wide. First femur, 5.8 mm; patella and tibia, 6.9 mm; metatarsus, 6.5 mm; tarsus, 1.6 mm. Second pa-

←

Plate 4. *Leucauge venusta* (Walckenaer); webs from Florida, diameter of viscid area about 28 cm. Upper web without spider; lower web with spider in hub. Web dusted with cornstarch.

tella and tibia, 4.9 mm; third, 2.0 mm; fourth, 3.5 mm.

Variation. Individuals have different amounts of black, red and yellow pigment. The ventral silver patches are most distinct in specimens from southern states, where another *Leucauge, L. argyra*, occurs (an example of character displacement). The ventral marks are often obliterated in more northern specimens. There is considerable variation in size in most collections. Total length of females, 3.7 to 8.0 mm. Carapace, 1.6 to 2.5 mm long, 1.2 to 1.9 mm wide; first patella and tibia, 3.4 to 5.5 mm long. Total length of males, 3.2 to 5.1 mm. Carapace, 1.6 to 2.2 mm long, 1.3 to 1.7 mm wide; first patella and tibia, 5.0 to 7.3 mm long. The degree of sclerotization of the epigynum varies, as does the relative length of the palpal tibia.

Diagnosis. Females can be separated from *L. argyra* north of Mexico by the subtriangular mark on the venter of the abdomen (Fig. 51, Plate 3) and by the shallow depression of the epigynum divided into three superficial parts (Figs. 45, 46). Males, unlike *L. argyra*, have a long palpal tibia, as long as or longer than the cymbium (Fig. 56), and lack a dorsal hook on the cymbium. Males can be separated from other tropical species by the shape of the conductor (Figs. 56, 57). Juveniles also have two silver triangular patches on the underside of the abdomen (Fig. 51), while those of *L. argyra* have two longitudinal lines. *Leucauge venusta* is often confused with *Mangora maculata*. *Mangora* has the trichobothria on the third patella and tibia, *Leucauge* on the fourth femur; the genitalia also differ.

Natural History. The webs have been described by Emerton (1902), Comstock (1913) and Kaston (1947). The webs are horizontal to near vertical with an irregular barrier web below. The orb has an open hub, about 30 or more radii, a wide free zone and more than 60 spirals (Plate 4). There are no scaffolding threads left in the web. The tip of the abdomen is in the center below the open hub, the first and second legs rest on the radii of the free zone, third and fourth on the mesh beyond the open hub. It is not known how often the web is remade and at what time of the day or night the spider spins. The webs are found in low bushes in wooded areas.

Males are found only from late May to early July in the northern part of the range, from April to June in Florida.

An egg-sac of *Leucauge venusta* from Virginia was made in June inside a collecting vial between a curled up leaf and the glass side, but only loosely attached to the glass. The egg-sac was made of loose, fluffy orange-white silk, was 8–9 mm in diameter (Plate 3) and contained several hundred eggs loosely stuck together, all reddish orange in color, each about 0.4 mm in diameter.

Distribution. Eastern United States (Map 3), New Hampshire to southeastern South Dakota to central Texas and south to Panama. Coast of California. Northernmost records are Hollis, New Hampshire, August 1888, ♀ (Fox) in the Museum of Comparative Zoology; Longvale, Mendocino County, California, June 1952, ♀ (W. J. Gertsch); and Supai, Havasu Canyon, Arizona, 2 April 1934, juv. (J. Lutz).

Leucauge argyra (Walckenaer)
Plate 5; Figures 60–71; Map 3

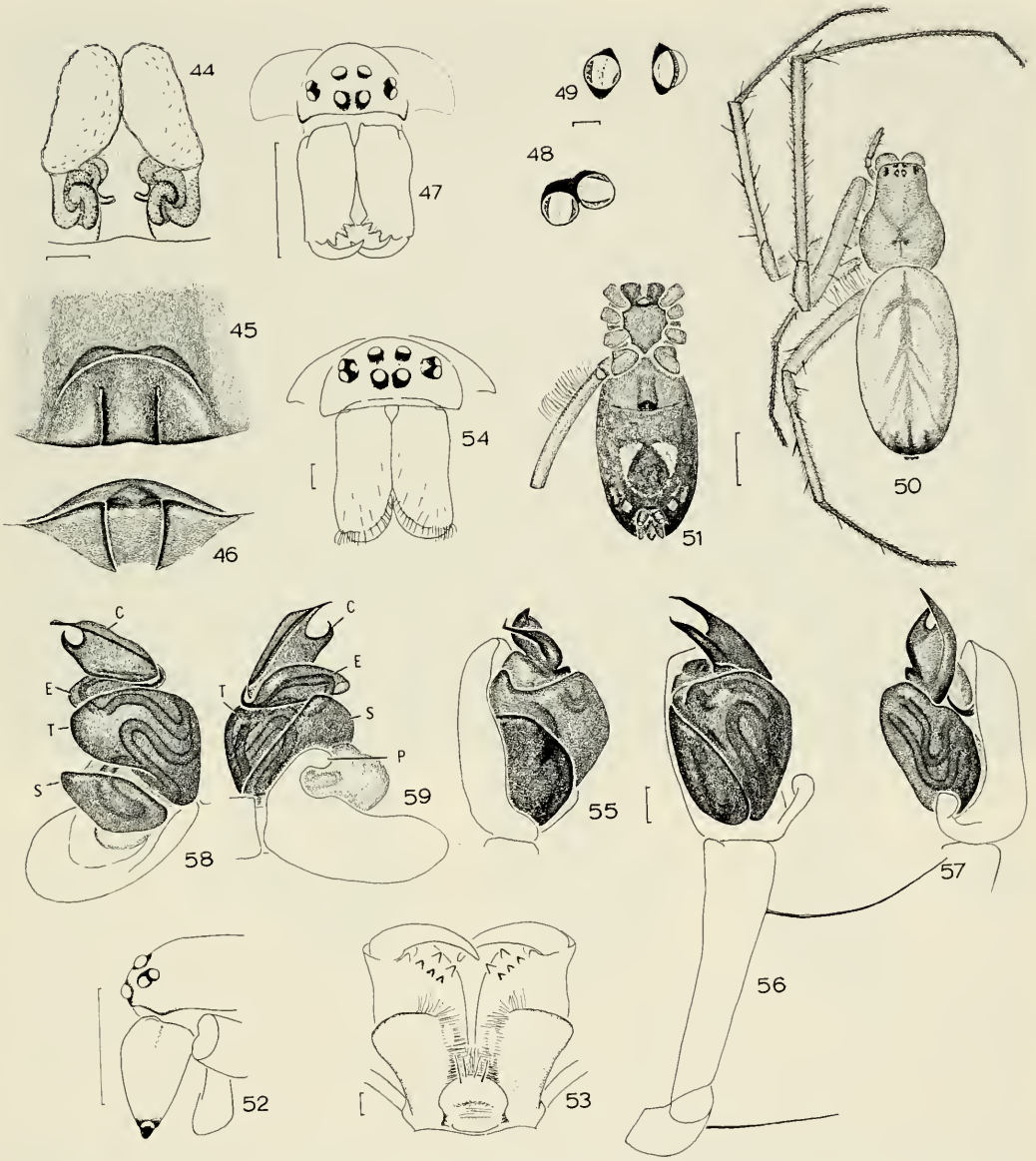
Tetragnatha argyra Walckenaer, 1841, Histoire Naturelle des Insectes Aptères, 2: 219, pl. 19, fig. 1, ♀. Walckenaer had specimens from Guadeloupe in the Antilles which are lost.

Linyphia aurulenta C. L. Koch, 1845, Die Arachniden, 12: 127, pl. 1049. Female from St. Thomas. DOUBTFUL NEW SYNONYMY.

?*Linyphia ornata* Taczanowski, 1874, Hor. Soc. Ent. Ross., 10: 66. Female from Cayenne and St. Laurent de Maron in French Guyana in the Polish Academy of Sciences, Warsaw.

Meta argyra:—Keyserling, 1880, Verhandl. Zool. Bot. Gesell. Wien, 30: 563, pl. 16, fig. 12, ♀, ♂.

Argyroepeira argyra:—McCook, 1893, American Spiders, 3: 243, pl. 24, figs. 2, 3. Keyserling, 1893, Spinnen Amerikas, 4: 343, pl. 18, fig. 253, ♀, ♂. Simon, 1894, Histoire Naturelle des Araignées, 1: 730, fig. 806, ♂.



Figures 44–59. *Leucauge venusta* (Walckenaer). 44–53. Female. 44–46. Epigynum. 44. Dorsal, cleared. 45. Ventral. 46. Posterior. 47. Eyes and chelicerae. 48. Left lateral eyes. 49. Posterior median eyes. 50. Dorsal. 51. Ventral. 52. Head and chelicera. 53. Labium and endites. 54–59. Male. 54. Eyes and chelicerae. 55–59. Left palpus. 55. Mesal. 56. Ventral. 57. Lateral. 58, 59. Expanded. 58. Ventral. 59. Dorsal.

Scale lines. 0.1 mm; Figures 47, 50–52, 1.0 mm.

Abbreviations. C, conductor; E, embolus; P, paracymbium; S, subtegulum; T, tegulum.

Plesiometa argyra:—F. P.-Cambridge, 1903, Biologia Centrali-Americana, Araneidea, 2: 438, pl. 41, figs. 15, 16, ♀, ♂. Comstock, 1912, *The Spider Book*, p. 424; 1942, rev. ed., p. 438. Bonnet, 1958, Bibliographia Araneorum, 2: 3709.

Leucauge argyra:—Petrunkevitch, 1930, Trans. Connecticut Acad. Sci., 30: 265, figs. 119, 120, ♀, ♂. Roewer, 1942, Katalog der Araneae, 1: 1009.

Note. *Liuyphia aurulenta* had previously been synonymized with *Leucauge venusta*. But Koch de-

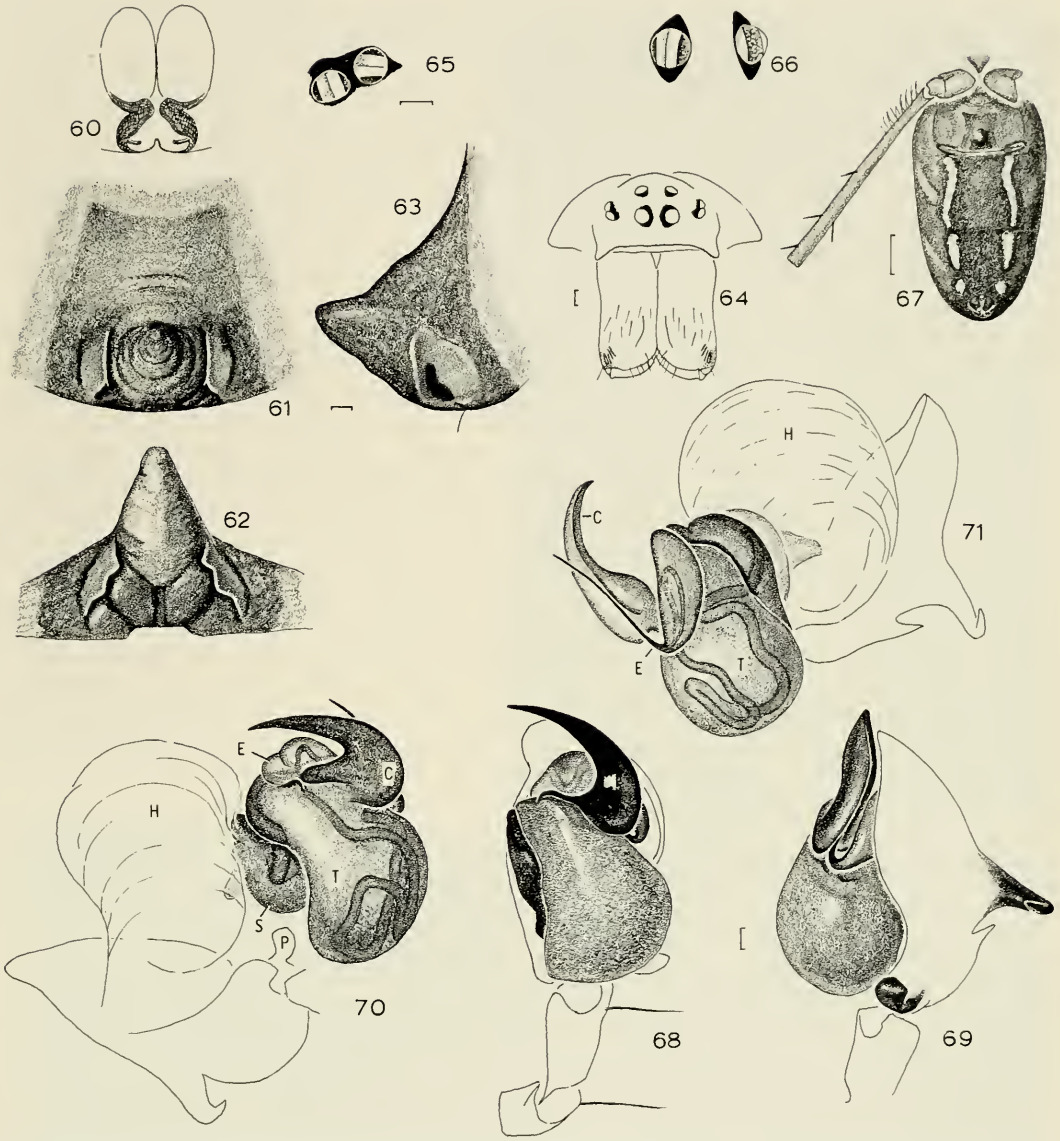
Plate 5. *Leucauge argyra* (Walckenaer), web from Puerto Rico, diameter about 50 cm (photo J. Coddington).

scribes the spider as having a black abdomen with golden marks, and the female as having cone-shaped genitalia. This cannot be *L. venusta*.

Description. Female from Florida. Carapace, sternum, legs orange-brown. Chelicerae dark brown distally, and sternum dark brown posteriorly. Dorsum of abdomen silvery, broken by median longitudinal and lateral lines and by branches radiating from the median line. Venter with two silver lines, one on each side, separated by brown and black pigment. Living specimens have orange-red patches (Fig. 67). The first and second legs have rows of denticles on the venter of tibiae and metatarsi. Total length, 9.1 mm. Carapace, 3.2 mm long, 2.3 mm wide. First femur, 8.0 mm long; patella and tibia, 8.8 mm; metatarsus, 8.8 mm; tarsus, 1.9 mm. Second patella and tibia, 6.4 mm; third, 2.4 mm; fourth, 4.8 mm.

Male from Florida. Coloration like female except silver patches are smaller. Legs with denticles as in female and palpal cymbium with a large, distally curved spine. Femur of palpus has a slight hump distally, facing widest place of endite. Total length, 6.6 mm. Carapace, 3.0 mm long, 2.3 mm wide. First femur, 8.4 mm; patella and tibia, 9.2 mm; metatarsus, 10.0 mm; tarsus, 2.3 mm. Second patella and tibia, 7.2 mm; third, 2.8 mm; fourth, 4.9 mm.

Variation. Individuals have a variable amount of black pigment. There is considerable variation in size. Females vary total length, 4.5 to 10.0 mm; carapace 1.9 to 3.6 mm long, 1.3 to 2.7 mm wide; first patella and tibia, 4.9 to 9.6 mm long. Males vary total length, 4.1 to 6.3 mm; car-



Figures 60–71. *Leucauge argyra* (Walckenaer). 60–67. Female. 60–63. Epigynum. 60. Dorsal, cleared. 61. Ventral. 62. Posterior. 63. Lateral. 64. Eye region and chelicerae. 65. Left lateral eyes. 66. Posterior median eyes. 67. Ventral. 68–71. Male left palpus. 68. Ventral. 69. Lateral. 70, 71. Expanded. 70. Ventral. 71. Dorsal.

Scale lines. 0.1 mm; Figure 67, 1.0 mm.

Abbreviations. C, conductor; E, embolus; H, hematodocha; P, paracymbium; S, subtegulum; T, tegulum.

apace, 1.9 to 3.0 mm long, 1.6 to 2.4 mm wide; first patella and tibia, 5.1 to 8.1 mm long.

Diagnosis. The female *L. argyra* is separated from all other species of *Leucauge* by the cone-shaped epigynum (Figs. 61–63), the male by the dorsal hook on the cymbium (Fig. 69) and the large sclerotized sickle-shaped conductor (Figs. 68, 70). Juveniles, unlike those of *L. ve-*

nusta, lack silver speckling between the two longitudinal ventral lines on the abdomen.

Natural History. *Leucauge argyra* makes a horizontal web in woods (Plate 5) and mangroves. It has been collected in sugar cane fields in Puerto Rico. Males have been collected in March, November and December in Florida.

Distribution. Central and southern Florida, Gulf Coast, West Indies, Mexico to South America, most abundant in the West Indies (Map 3).

Metellina Chamberlin and Ivie

Metellina Chamberlin and Ivie, 1941, Bull. Univ. Utah, biol. ser., 6(3): 14. Type species *Metellina curtisi* (McCook) by original designation. The generic name is feminine.

Diagnosis. Unlike *Meta* and *Metleucauge*, the *Metellina* abdomen is longer than wide, dorsoventrally slightly flattened, widest anteriorly sometimes with small humps (Fig. 75). The venter has a median longitudinal black band with a white line on each side (Fig. 76). Unlike tropical *Chrysometa*, there are no silver spots on the abdomen. The chelicerae have only 3 teeth on the posterior margin (Fig. 74, 88); *Meta* and *Metleucauge* have four.

The male and female genitalia are weakly sclerotized compared to those of *Meta* and *Metleucauge*. The epigynum has at most a simple depression with a lightly sclerotized lip containing the openings on the ventral surface (Figs. 78, 90, 102, 109). The paracymbium of the male palpus is lightly sclerotized (Figs. 84, 92, 104, 107, 111), as are the conductor and base of embolus (C, E in Figs. 99, 100, 104, 111). Unlike the tropical *Chrysometa* the lateral side of the cymbium is not divided, lobed or indented (Figs. 85, 93), except for the basal paracymbium.

Description. Carapace yellow-white to light brown with gray to brown patches, eye area light without median line; sometimes V-shaped marks (Fig. 75). Sternum black (Fig. 76). Coxae and other leg articles yellow-white, more or less distinctly banded (Fig. 75). Dorsum of abdomen white with paired black patches, patches widest apart anteriorly, more distinct but closer together posteriorly (Fig. 75). Venter with a median longitudinal black band, bordered on each side by a white band (Fig. 76); spinnerets and ring surrounding them dark with two white spots on each side (Fig. 76).

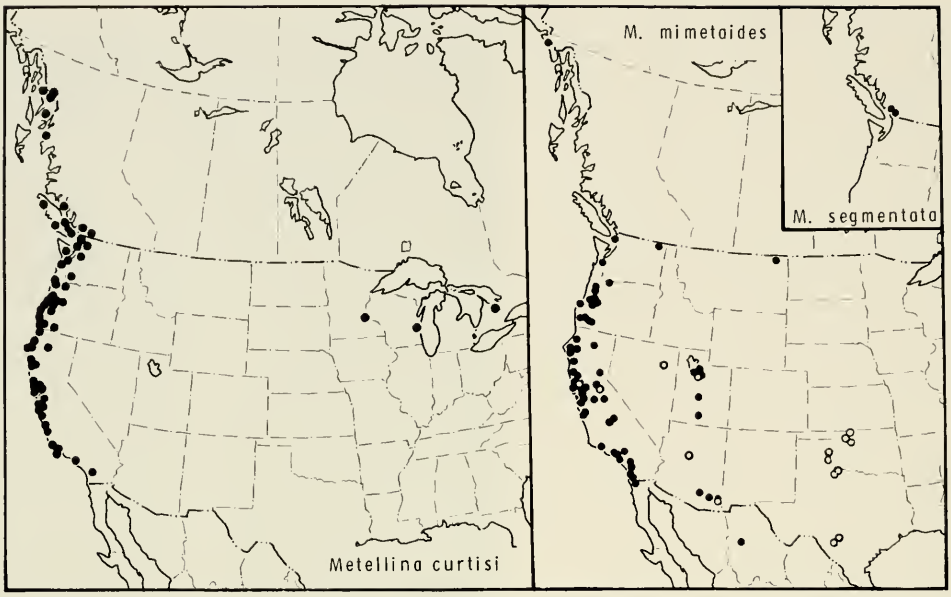
Carapace is narrow in front, eyes are closely grouped (Figs. 72, 73, 75). Height of clypeus equals diameter of anterior median eyes. Eyes subequal in size, anterior medians sometimes very slightly larger or smaller than others (Figs. 72, 73, 87). Anterior median eyes their diameter apart, 1.3 to 2 diameters from laterals. Posterior median eyes about their diameter apart and the same distance to 1.5 diameters from laterals. Secondary eyes with canoe tapetum (Figs. 95, 96). Chelicerae fairly strong; three large teeth on anterior margin, three on posterior, the middle one small (Figs. 74, 88). Endites longer than wide, widest distally (Fig. 76). First leg longest, second next, third shortest. Abdomen oval, dorsoventrally slightly flattened, widest anteriorly (Fig. 75).

Short trichobothria are on palpi, leg tibiae and metatarsi, none on femur. The tibiae have 6 to 8 trichobothria widely spaced dorsally, and one trichobothrium dorsally on base of metatarsus.

Males may be larger than females (*M. curtisi*) or only slightly smaller than females; the chelicerae may be enlarged (*M. curtisi*). Males have narrower abdomen. They lack the tooth on the proximal end of the palpal femur and its matching

→

Plate 6. *Metellina curtisi* (McCook). Upper photograph female; lower one web, about 15 cm diameter (lower photo by D. J. Boe).



Map 4. Distribution of *Metellina curtisi* (McCook), *Metellina mimetoides* Chamberlin and Ivie and American distribution of *M. segmentata* (Clerck). Open circles are cave records of *M. mimetoides*.

tooth on the endite. None of coxae or legs are modified.

Genitalia. The female epigynum has a lightly sclerotized median ventral depression (Figs. 78, 90, 102, 106, 109) with lateral openings leading into heavily sclerotized seminal receptacles (Figs. 77, 79, 89, 101, 105, 108). Although Wiehle (1967) could not find fertilization ducts in the *Meta* group of species (examined by sectioning the spiders), I think there are such ducts, but the lightly sclerotized flattened ducts may be difficult to discern.

The male palpi are also lightly sclerotized. The conductor (C in Figs. 99, 100) is a lobe from the tegulum supporting the distal part of the embolus (E); the base of the embolus is also a lightly sclerotized, almost spherical lobe. The paracymbium is large and has two branches (Figs. 84, 92, 104, 107, 111).

Species. The species, except European *M. merianae*, are difficult to separate. I know of only 5: *M. merianae*, *M. mengei* and *M. segmentata* in Eurasia; *M. curtisi* and *M. mimetoides* in western North America. The Eurasian *M. segmentata* is introduced in British Columbia.

Natural History. The species have a near vertical web with an open hub (Plate 6). The American species are found in dark humid situations and *M. mimetoides* is common in caves.

KEY TO *METELLINA* SPECIES NORTH OF MEXICO

1. Females 2
– Males 4
2(1). Epigynum with a median, bordered depression (Figs. 78, 80, 82, 90) 3
– Epigynum with pair of shallow unbordered depressions (Fig. 102); British Columbia ..... *segmentata*
3(2). Depression usually without median septum; width of depression about 1.2 times length (Figs. 78, 80, 82) ..... *curtisi*
– Depression with median septum and width of depression about 2.5 times length (Fig. 90) ..... *mimetoides*
4(1). Tibia of male palpus (when in ventral view) hardly longer than wide (Figs. 91, 92) ..... *mimetoides*
– Tibia of male palpus distinctly longer than wide (Figs. 83, 84, 104) 5

5(4). Conductor in ventral view in transverse position with distal edge shallow, concave (Fig. 104); British Columbia ---- *segmentata*

– Conductor in ventral view in transverse and mesal position, distal edge strongly concave (Fig. 84) ---- *curtisi*

Metellina curtisi (McCook)

Plate 6; Figures 72–86; 95–98; Map 4

Epeira peckhamii McCook, 1893, American Spiders, 3: 189, pl. 18, figs. 5, 6, ♀, ♂. Male, female from Biscayne Bay, Florida (G. Marx) [locality in error] and Wisconsin (G. Peckham). Two female syntypes in Academy of Natural Sciences, Philadelphia, examined. NEW SYNONYMY.

Pachygnatha curtisi McCook, 1893, American Spiders, 3: 271, pl. 26, fig. 5, ♂. Fragments of 3 male syntypes from California in the Academy of Natural Sciences, Philadelphia, examined and labeled as types.

Meta curtisi:—Gertsch and Ivie, 1936, Amer. Mus. Novitates, 858:20.

Metellina curtisi:—Chamberlin and Ivie, 1941, Bull. Univ. Utah, biol. ser., 6(3): 15, fig. 20, ♀.

Note. The illustration of the male *E. peckhami* is doubtless this species. The epigynum illustrated does not fit, the body of the female illustrated does, and so do the two surviving specimens. Since the species has been cited in the literature as *M. curtisi* I will keep this name, although *E. peckhami* has page priority. According to ICZN Art. 24, the first reviser can choose the name that provides most stability.

In collections, specimens had been erroneously determined as *Cyrtophora californiensis* by Banks and Chamberlin; *C. californiensis* Keyserling is a *Eustala*.

Description. Female from Oregon. Total length, 5.0 mm. Carapace, 1.9 mm long, 1.5 mm wide. First femur, 2.5 mm; patella and tibia, 3.3 mm; metatarsus, 2.4 mm; tarsus, 1.2 mm. Second patella and tibia, 2.5 mm; third, 1.3 mm; fourth, 1.9 mm.

Male from Oregon. Chelicerae enlarged (Figs. 73, 74). Three teeth on anterior margin; on posterior one large tooth near base of fang and two additional smaller teeth (Fig. 74). Total length, 4.3 mm. Carapace, 2.2 mm long, 1.6 mm wide. First femur, 4.0 mm; patella and tibia, 5.3 mm; metatarsus, 4.2 mm; tarsus, 1.7 mm. Second patella and tibia, 3.8 mm; third, 1.8 mm; fourth, 2.6 mm.

Variation. Males are generally slightly larger than females. Total length of females, 3.4 to 5.5 mm; carapace, 1.4 to 2.3 mm long, 1.2 to 1.7 mm wide; first patella and tibia, 2.7 to 3.7 mm long. The largest specimen came from Alaska. Males 4.0 to 7.3 mm total length; carapace, 1.8 to 3.0 mm long, 1.5 to 2.1 mm wide; first patella and tibia, 4.5 to 8.0 mm long.

Diagnosis. Metellina curtisi female differs from *M. mimetoides* in the shape of the epigynum, a depression hardly wider than long (Figs. 78, 80, 82). The male has the palpal tibia about twice as long as wide (Figs. 83, 84), unlike *M. mimetoides*, which has the tibia hardly longer than wide.

Natural History. Adult females have been found from January to September; males from January to August, most common in April to July. Adults disappear in fall and early winter in Oregon and California. Females are adult in September in Alaska. Collecting sites are: walls of shed and shrubs in British Columbia, rain forest in Washington, and in redwood forest in Oregon and California. Other specimens have been collected in insect flight trap, in dense forest; small webs near ground among shrubs and grasses. Don J. Boe (personal communication) observed webs in relatively dark places, out of sunlight, near water 23 miles north of Santa Barbara, and Big Sur, California 60 to 250 cm above ground. The webs were 10 to 18 cm diameter and 0 to 10° from vertical. One web was horizontal, had 19 to 25 radii, 11 to 19 spirals above, and 15 to 23 below the hub. The hub is open (Plate 6).

Distribution. Pacific coast from southern Alaska to southern California (Map 4). The southernmost record is from San Jacinto Mts., Riverside County, California, August 1958 (E. I. Schlinger); other unusual records are Minneapolis, Minnesota, November 1930, ♀ (W. J. Gertsch); Wisconsin, syntypes of *M. peckhami* (G. W. Peckham); and Horn-

ings Mills, Ontario, 19 June 1927, ♀ (T. B. Kurata).

Metellina mimetoides Chamberlin and Ivie

Figures 87–94; Map 4

Metellina mimetoides Chamberlin and Ivie, 1941, Bull. Univ. Utah, biol. ser., 6(3): 15, fig. 19, ♀. Female holotype from Mount Diablo, California, in the American Museum of Natural History, lost.

Note. Some specimens of this species had been determined as *Cyrtophora californiensis* by Banks.

Description. Female. Female has more black pigment than *Metellina curtisi*. Total length, 5.0 mm. Carapace, 1.8 mm long, 1.5 mm wide. First femur, 2.4 mm; patella and tibia, 3.3 mm; metatarsus, 2.4 mm; tarsus, 1.0 mm. Second patella and tibia, 2.7 mm; third, 1.3 mm; fourth, 1.9 mm.

Male. The chelicerae of the male are smaller than those of the male of *M. curtisi* (Figs. 87, 88). Total length, 3.8 mm. Carapace, 1.9 mm long, 1.6 mm wide. First femur, 3.3 mm long; patella and tibia, 4.1 mm; metatarsus, 3.5 mm; tarsus, 0.9 mm. Second patella and tibia, 3.2 mm; third, 1.5 mm; fourth, 2.0 mm.

Variation. Total length of females, 3.3 to 6.0 mm. Carapace, 1.6 to 2.7 mm long, 1.2 to 2.0 mm wide; first patella and tibia, 2.6 to 4.3 mm long. Total length of males, 3.1 to 4.9 mm. Carapace, 1.5 to 2.4 mm long, 1.2 to 1.9 mm wide; first patella and tibia, 3.0 to 5.2 mm long. All the largest specimens came from caves of the eastern part of the range of the species. Unlike *M. curtisi*, the males are slightly smaller than females and there is much less variation in size.

Diagnosis. Metellina mimetoides female has a septum in the epigynum depression, the sides of the depression directed laterally. The total width of the depression is more than twice its length (Fig. 90). Unlike *M. curtisi*, the male has the palpal tibia hardly longer than wide (Figs. 91, 92), while that of *M. curtisi* is about twice as long as wide. The male chelicerae are not much longer than those of the females and have three equally spaced teeth (Figs. 87, 88); in *M. curtisi* the chelicerae are much larger and the space between the distal teeth is wider than the space between the proximal. Both sexes are more pigmented and the markings more contrasting than those of *M. curtisi*.

Natural History. This species has been found in webs on woodpiles and in shacks, aboard ship in a Los Angeles dock, under an overhanging rock ledge, and in oak-grassland in the Santa Catalina Mountains, Arizona. Many of the easternmost records of this species come from caves (open circles, Map 4). The males are commonly collected while sweeping vegetation. I suspect its habitat is similar to *M. curtisi*, but its distribution is more southern.

Distribution. From southern Alaska, Pacific coast to northern Baja California, as far west as Utah and in caves from Nevada to Oklahoma, Texas to Sonora (Map 4).

Metellina segmentata (Clerck)

Figures 99–104; Map 4

Araneus segmentatus Clerck, 1757, Aranei Suecici, p. 45, pl. 2, fig. 6, ♀, ♂. Female and male specimens from Sweden.

Aranea reticulata Linnaeus, 1758, Systema Naturae, p. 619. Specimens from Sweden.

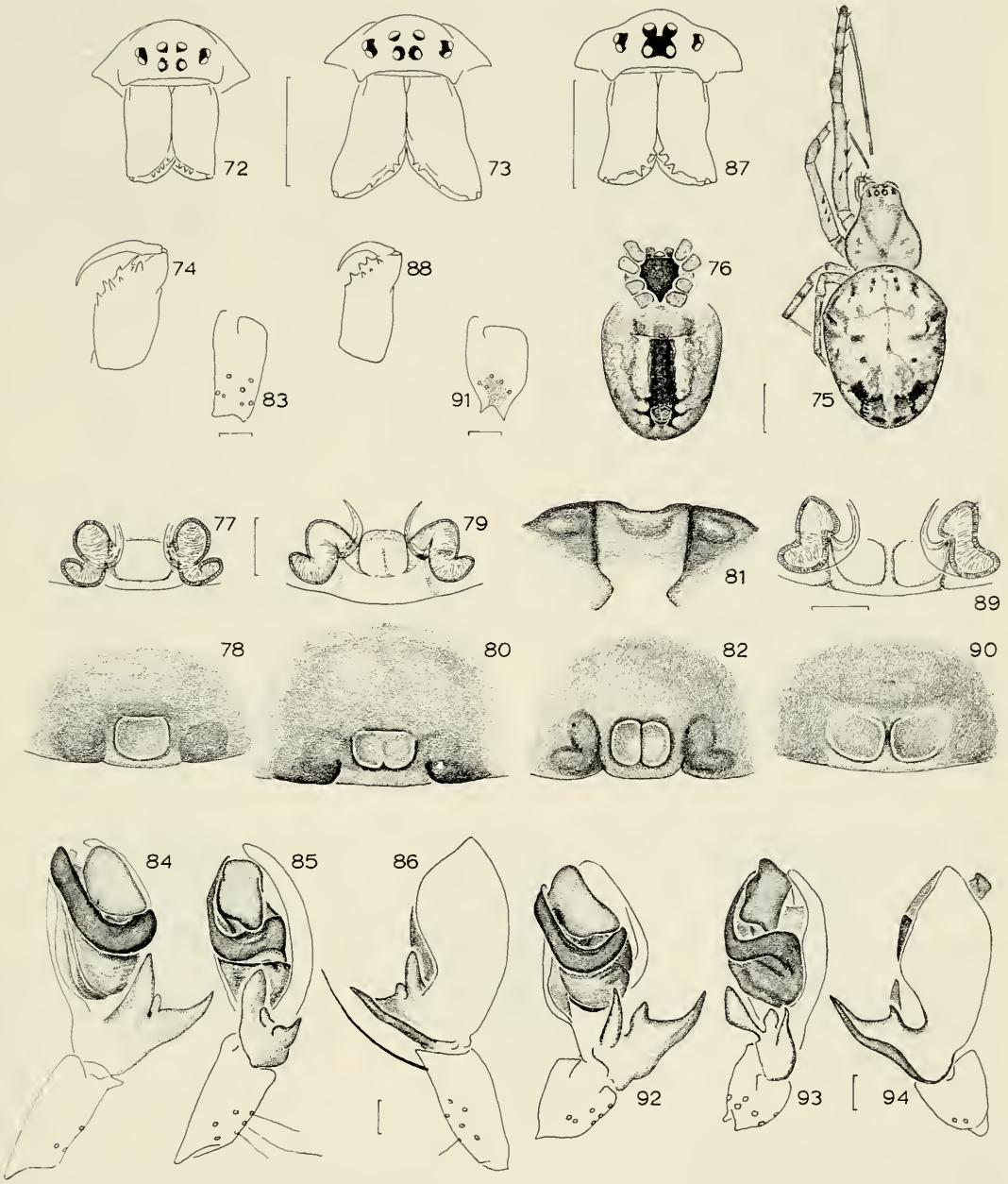
Meta reticulata:—Wiehle, 1931 in Dahl, Tierwelt Deutschlands, 23: 119, figs. 192–197, ♀, ♂. Roewer, 1942, Katalog der Araneae, 2: 915.

Meta segmentata:—Locket and Millidge, 1953, British Spiders, 2: 115, figs. 75, 76B, 77A, D. Bonnet, 1957, Bibliographia Araneorum, 2(3): 2797. Locket, Millidge and Merrett, 1974, British Spiders, 3: 64, figs. 36a, 37b,d, ♀, ♂.

Note. All older North American records are from misidentified specimens of the two native species.

Diagnosis. Metellina segmentata differs from the two other North American species by lacking a bordered depression in the epigynum (Fig. 102) and by having a wide palpal conductor in transverse position (Fig. 104).

This species can be separated from the European *M. mengei* (Figs. 105–107) by the structure of the seminal receptacles and the shorter length of the palpal embolus (Figs. 101, 104). The embolus seen



Figures 72–86. *Metellina curtisi* (McCook). 72, 73. Eye region and chelicerae. 72. Female. 73. Male. 74. Male chelicera, posterior view. 75, 76, Female. 75. Dorsal. 76. Ventral. 77–82. Epigynum. 77, 79. Dorsal cleared. 78, 80, 82. Ventral. 81. Posterior. 77, 78. (Mendocino County, California). 79–81. (Yamhill County, Oregon). 82. (Friday Harbor, Washington). 83–86. Left palpus; 83. Tibia, lateral. 84. Ventral. 85. Lateral. 86. Dorsal.

Figures 87–94. *M. mimetoides* Chamberlin and Ivie. 87. Male eye region and chelicerae. 88. Male chelicera, posterior view. 89, 90. Epigynum. 89. Dorsal, cleared. 90. Ventral. 91–94. Palpus. 91. Tibia, lateral. 92. Ventral. 93. Lateral. 94. Dorsal.

Scale lines. 0.1 mm; Figures 72–76, 87, 88, 1.0 mm.

through the semitransparent conductor (turning and shifting may be necessary) is longer in *M. mengei* (Fig. 107) than in *M. segmentata* (Fig. 104). The ventral lobe of the lateral prong of the paracymbium is more distinct in *M. mengei* (Fig. 107) than in *M. segmentata* (Fig. 104).

There is little variation of appearance of the epigynum of *M. segmentata* (Figs. 102, 103), but considerable variation in the European *M. mengei* (Figs. 105, 106). Usually the anterior, slightly more dorsal lobe of the seminal receptacle is visible as a distinct lobe through the translucent epigynum in *M. segmentata* (Fig. 102). This lobe is more posterior and dorsal in *M. mengei*, and there appears to be one elongate seminal receptacle on each side. If there is doubt, clearing or dissection may be needed to see differences of the seminal receptacles in dorsal view (Figs. 101, 105).

Natural History. *Metellina segmentata* is not native to North America; it is introduced in the Vancouver area. Habits are reported in Wiehle (1931) and Locket and Millidge (1953).

Records. British Columbia. Vancouver, 24 Sept. 1966, 1♀; 18 Oct. 1969, 1♂, beaten from bushes (P.D.B., R. Leech collection); Surrey, Fraser Valley, 18 September 1976, 3♀, wooded area (J. Stafford, MCZ collection).

Meta C. L. Koch

Meta C. L. Koch, 1836, Arachniden in Panzer, Faunae Insectorum Germaniae initia, Heft 134, pl. 12. Type species by original designation *Meta fusca* Walckenaer (=*Meta menardi*). The name is feminine.

Diagnosis. Unlike *Metellina* and *Metleucauge*, the *Meta* abdomen is almost as high as long, in appearance like that of the theridiid *Achaearanea* (Figs. 113–115).

The epigynum has a median swelling with openings posterior (Figs. 117–119, 129), unlike that of *Metellina* and *Metleucauge*, which have the openings ventral. Both the conductor and the embolus are sclerotized, unlike those of *Metellina* species, and the base of the embolus is a complex dissected sclerite with lobes and apophyses (E in Figs. 124, 125).

Description. Carapace glossy brown; thorax lighter than head (Fig. 114). Chelicerae dark brown. Legs brown, usually indistinctly banded darker. Dorsum of abdomen with paired dark patches and scattered white pigment spots on brown to gray background; posteriorly darker with transverse light bars; sides streaked (Figs. 113, 114). Venter gray to black, quite variable, usually with two longitudinal light bands consisting of tiny white pigment spots. Carapace narrow in head region and eyes closely spaced (Fig. 112, 114). Height of clypeus equals 1.2 to 1.5 diameters of anterior median eyes (Fig. 112). Eyes subequal in size, sometimes secondary eyes slightly larger than anterior medians. Anterior median eyes slightly less than their diameter apart, 1.2 to 1.5 from laterals; posterior median eyes slightly less than their diameter apart, about 1.5 from laterals. Secondary

→

Figures 95–98. *Metellina curtisi* (McCook). 95. Left lateral eyes. 96. Posterior median eyes. 97, 98. Left palpus, expanded. 97. Ventral. 98. Subdorsal.

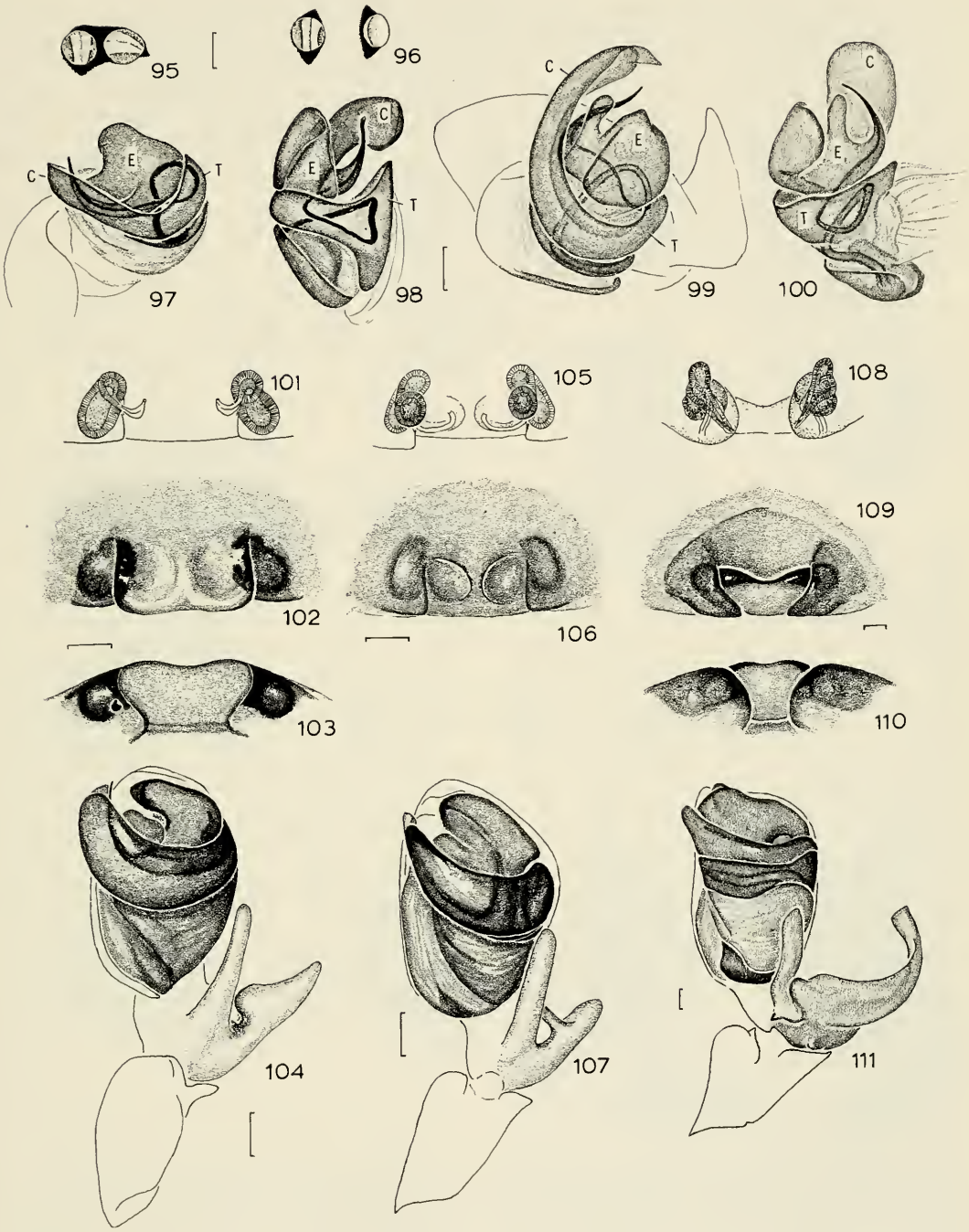
Figures 99–104. *M. segmentata* (Clerck). 99, 100. Left palpus, expanded. 99. Ventral. 100. Dorsal. 101–103. Epigynum. 101. Dorsal, cleared. 102. Ventral. 103. Posterior. 104. Left male palpus, ventral.

Figures 105–107. *M. mengei* (Blackwall) of Europe. 105, 106. Epigynum. 105. Dorsal, cleared. 106. Ventral. 107. Palpus, ventral.

Figures 108–111. *M. merianae* (Scopoli) of Europe. 108–110. Epigynum. 108. Dorsal, cleared. 109. Ventral. 110. Posterior. 111. Palpus, ventral.

Scale lines. 0.1 mm.

Abbreviations. C, conductor; E, embolus; T, tegulum.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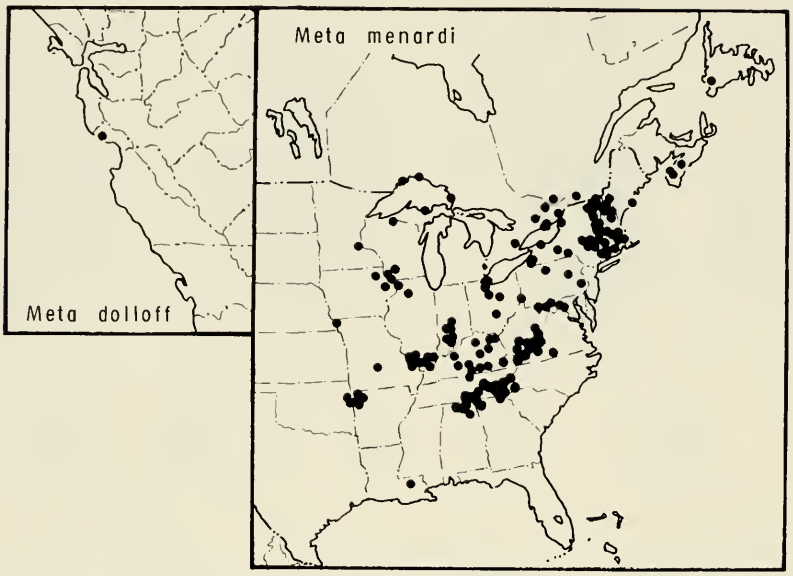


Map 5. Distribution of *Meta dolloff* new species and American distribution of *M. menardi* (Latreille).

eyes with canoe tapetum (Figs. 122, 123). Chelicerae with 3 teeth on anterior margin, 4 on posterior. Endites wider on distal end than on proximal end (Fig. 121). First legs longest, second next, third shortest. Abdomen about as high as long, widest in middle (Figs. 113–115).

No trichobothria on femora, two rows of trichobothria on dorsum of proximal half of tibia (altogether 5 or 6). The first three legs (of *Meta menardi*) have a single dorsal trichobothrium on proximal end of metatarsus.

Males are slightly smaller than females. The chelicerae have a larger anterior hump at their bases and are more curved distally. They lack the tooth on the proximal end of the palpal femur and its counterpart on the endite, which is present in species of *Araneus*. No coxae or legs are modified.

Genitalia. The epigynum has a median ventral lobe, hairy in *Meta menardi* (hairs not shown in Figs. 117–119). The openings are on the posterior face (Figs. 118–120). According to Wiehle (1967) there are no separate fertilization ducts. Wiehle made sections; I am uncertain if this is right as I could not verify it.

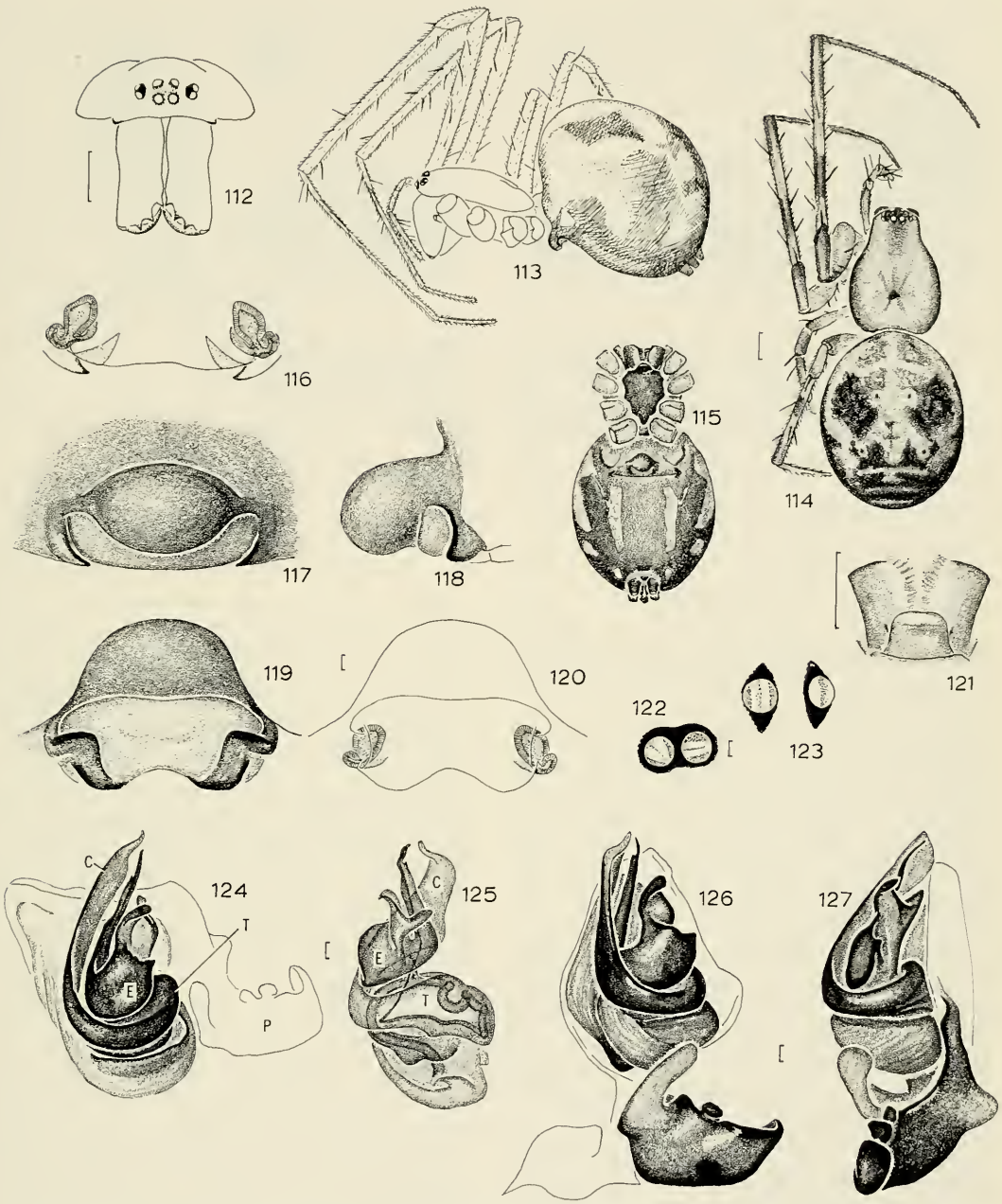
The palpus is sclerotized. The conductor (C in Figs. 124, 125), a lobe of the tegulum, holds the filamentous part of the embolus (E). The embolus has a dissected sclerotized base of different shape in different species. The paracymbium (P) is very large, lobed and sclerotized.

Species. Species of *Meta* are probably world-wide. There are only two in North America: *Meta menardi* and *Meta dolloff*.

Natural History. Meta species are found in dark places, and are common in caves. The orb-web is vertical with an open hub.

Key to Species of *Meta* North of Mexico

1. Epigynum with a median notch in anterior swelling (Fig. 133); palpal conductor with a distal lobe (Fig. 135); paracymbium with a lateral finger (Fig. 135); California caves (Map 5) ..... *dolloff*
– Epigynum with a median, anterior, rounded, hairy swelling (Figs. 117–119); palpal conductor with narrowed tip at an angle (Figs. 124, 126); paracymbium in ventral



Figures 112–127. *Meta menardi* (Latreille). 112–123. Female. 112. Eye region and chelicerae. 113. Lateral. 114. Dorsal. 115. Ventral. 116–120. Epigynum. 116. Dorsal, cleared. 117. Ventral. 118. Lateral. 119. Posterior. 120. Posterior, cleared. 121. Labium and endites. 122. Left lateral eyes. 123. Posterior median eyes. 124–127. Left male palpus. 124. Expanded, ventral. 125. Expanded, lateral. 126. Ventral. 127. Lateral.

Scale lines. 0.1 mm; Figures 112–115, 121, 1.0 mm.

Abbreviations. C, conductor; E, embolus; P, paracymbium; T, tegulum.

view with a keel laterally (Figs. 124, 126); eastern North America, cave-dwelling and epigean (Map 5) ..... *menardi*

Meta menardi (Latreille)
Figures 112–127; Map 5

Aranea menardii Latreille, 1804, Histoire Naturelle Générale des Crustacés et des Insectes, 7: 266. Specimens described from le Mans, France, lost.

Meta menardi:—Thorell, 1870, Rem. Syst. Europ. Spiders, p. 38. Emerton, 1884, Trans. Connecticut Acad. Sci., 6: 328, pl. 34, fig. 18, pl. 37, fig. 33, ♀, ♂. McCook, 1893, American Spiders, 3: 246, pl. 22, figs. 4, 5, ♀, ♂. Keyserling, 1893, Spinnen Amerikas, 4: 313, pl. 16, fig. 231, ♀, ♂. Emerton, 1902, Common Spiders, p. 190, figs. 443–445, ♀, ♂. Wiehle, 1927, Z. Morphol. Ökol. Tiere, 8: 513, web. Wiehle, 1931, in Dahl, Tierwelt Deutschlands, 23: 128, figs. 4c, 5b, 205–209, ♀, ♂. Nielsen, 1932, Biology of Spiders, 2: 502, figs. 344–346, webs, egg-sacs. Comstock, 1940, Spider Book, rev. ed., p. 433, figs. 431–433, ♀, ♂, egg-sac. Roewer, 1942, Katalog der Araneae, 1: 916. Kaston, 1948, Bull. Connecticut Geol. Natur. Hist. Surv., 70: 223, figs. 700–703, ♀, ♂. Locket and Millidge, 1953, British Spiders, 2: 119, figs. 78, B, C, ♀, ♂. Bonnet, P., 1957, Bibliographia Araneorum, 2: 2787.

Description. Female. Epigynum has a median hairy bulge (hairs not shown in Fig. 117). Total length, 12.5 mm. Carapace, 5.8 mm long, 4.5 mm wide. First femur, 8.9 mm; patella and tibia, 11.2 mm; metatarsus, 9.0 mm; tarsus, 3.0 mm. Second patella and tibia, 9.4 mm; third, 6.1 mm; fourth, 7.8 mm.

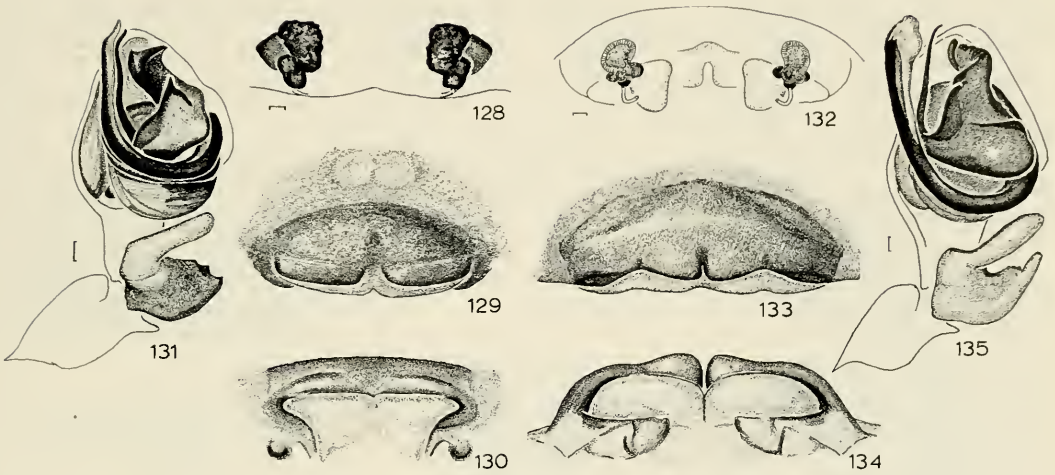
Male. The abdomen is more elongate than that of female. Total length, 10.0 mm. Carapace, 5.0 mm long, 3.7 mm wide. First femur, 8.1 mm; patella and tibia, 10.4 mm; metatarsus, 8.8 mm; tarsus, 2.9 mm. Second patella and tibia, 8.2 mm; third, 4.9 mm; fourth, 6.3 mm.

Variation. Females vary in size from 7.8 to 13.7 mm total length; carapace, 4.0 to 5.9 mm long, 3.3 to 4.5 mm wide, first patella and tibia, 8.2 to 11.5 mm long. Males vary in size from 7.0 to 10.1 mm total length; carapace, 3.7 to 5.2 mm long, 3.0 to 4.0 mm wide; first patella and tibia, 8.3 to 11.6 mm long.

Diagnosis. *Meta menardi* females differ from *M. dolloff* and from other species by the median swollen bulge of the epigynum (Fig. 117); the bulge is hairy (not shown in illustrations). The male differs from *M. dolloff* and other species by the shape of the huge median apophyses (P in Figs. 124, 126). Juveniles can generally be identified by the abdominal markings: a pair of anterior, dorsal dark patches (Figs. 113, 114) together with two ventral parallel light lines (Fig. 115). The only other species of *Meta* in North America, *M. dolloff*, is found in California. *Meta* has been confused with *Zygiella*. But the dorsal abdominal pattern of *Zygiella* species is always different, more like that of *Metleucauge*.

Natural History. Many specimens in collections come from deep within caves, around the mouth of caves, and from old mines and wells; but the species is also found in dark ravines, under overhanging rocks, and sometimes in cool cellars. Males and females appear mature at all seasons. The web is at a slight angle from the vertical, to horizontal. Kaston (1948) reports 8 to 18 radii in an orb 15 to 30 cm across. The hub is open. The spider hangs in the hub or at the end of a trap-line under a nearby rock. The egg-sac is large, white, drop-shaped, fluffy and translucent, about 20 mm long. It hangs on a thread near the web; it is pictured in Comstock (1940). Wiehle (1931) believes that this species takes at least two years to mature.

Distribution. Judging from its habitat, the species is probably native. Eurasia, eastern Canada and United States (Map 5) from Newfoundland to Minnesota, eastern Oklahoma and south along the Appalachian Mountains. The westernmost localities are a cave near Rock Port, Atchison Co., Missouri, 6 November 1904, 30 December 1904 (C. R. Crosby, Cornell Univ. Coll.), Three Forks Cave, Gittin Down Mountain, Adair Co., Oklahoma, 1 August 1959, ♀ (J. Black, AMNH); southernmost is Baton Rouge, Louisiana (Gibbeau, Cornell Univ. Coll.).



Figures 128–131. *Meta bourneti* Simon (Mediterranean). 128–130. Epigynum. 128. Dorsal, cleared. 129. Ventral. 130. Posterior. 131. Left male palpus.

Figures 132–135. *M. dolloff* new species. 132–134. Epigynum. 132. Dorsal, cleared. 133. Ventral. 134. Posterior. 135. Left palpus.

Scale lines. 0.1 mm.

Meta dolloff new species
Figures 132–135; Map 5

Pseudometa biologica:—Graham, 1967, Caves and Karst, 9: 17. Not *P. biologica* Chamberlin (=*Zygiella x-notata*).

Holotype. Male holotype from Empire Cave, Santa Cruz Co., California, 26 August 1963 (R. Graham), in the American Museum of Natural History. The specific name is a noun in apposition after one of the localities.

Description. Female paratype. Carapace, sternum, labium brown. Coloration much like *Meta menardi*, leg banding less distinct. Dorsum of abdomen anteriorly with a pair of dark patches; in between patches are two light triangles, pointing anteriorly, one after the other; posteriorly abdomen has dark transverse bars. Sides streaked. Venter has two parallel light lines on dark gray. Head region of carapace very narrow; thoracic depression a deep pit. Eyes subequal in size. Anterior median eyes slightly less than their diameter apart, 1.3 from laterals. Posterior medians their diameter apart, 1.4 from laterals. Chelicerae very strong, with a basal boss. Three teeth on anterior margin, two together near base of fang. Posterior margin with three teeth close to fang, one more distal. Total length, 14.0 mm. Carapace, 6.3 mm wide, 5.0 mm long. First femur, 9.6 mm long; patella and tibia, 12.9 mm; metatarsus, 10.3 mm; tarsus, 3.5 mm. Second patella and tibia, 10.2 mm; third, 6.6 mm; fourth, 9.0 mm.

Male. Coloration, eye placement and cheliceral teeth as in female. Total length, 11.0 mm. Carapace, 5.9 mm long, 4.5 mm wide. First femur, 10.2 mm long; patella and tibia, 13.3 mm; metatarsus, 11.7 mm; tarsus, 3.2 mm. Second patella and tibia, 10.6 mm long; third, 6.2 mm; fourth, 7.9 mm.

Diagnosis. Meta dolloff females, unlike those of *Meta menardi*, have a median notch at the anterior lip of the epigynum (Fig. 133). The notch is narrower than that of *M. bourneti* (Fig. 129). The paracymbium of the male palpus has a large ventral finger and a smaller lateral one (Fig. 135), while that of *M. bourneti* (Fig. 131) and *M. menardi* (Fig. 126) has only a ventral one. The structure of the distal projection of the base of the em-

bolus, the tip of embolus, and the conductor also differ from the two other species.

Distribution. The only specimens seen come from two caves in Santa Cruz County, California. A nearby cave in Santa Cruz County is known as the Cave of the Dancing Spiders, but no spiders are available from it. It is of interest that this species is very close to *Meta bourneti* (Figs. 128–131) of the Mediterranean region.

Records. Paratypes. *California.* Santa Cruz Co.: Empire Cave, Sect. 3, T11S, R3W, Santa Cruz Quadr., 26 Aug. 1963, 3 ♀ (R. Graham); Dolloff Cave, Sect. 3, T11S, R3W, Santa Cruz Quadr., 28 Aug. 1963, ♀ (R. Graham).

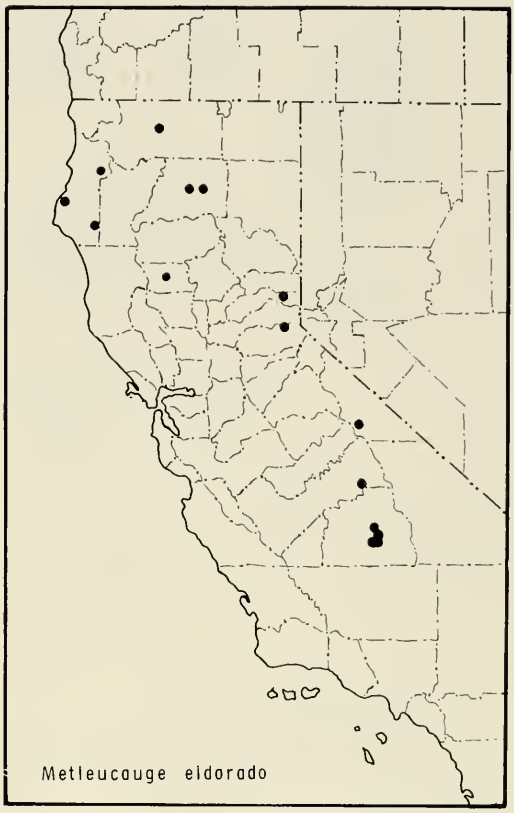
Metleucauge new genus

Type species. Metleucauge eldorado. The generic name is feminine.

Diagnosis. The abdomen, unlike that of *Metellina* and *Meta* species, is ovoid, dorsoventrally flattened, and widest in the middle (Figs. 142, 143). The epigynum is a flat sclerotized structure, unlike that of *Meta* and *Metellina*, and has pockets on the sides of the venter (Figs. 137, 138). Unlike those of related genera, the articles of the palpus are elongated, and the palpal trochanter has a distal spur (Figs. 145, 151). The paracymbium is reduced (P in Figs. 146, 147, 149); the large tegulum shows the coiled duct, resembling *Leucauge* species; and the expanded palpus shows the presence of conductor, embolus and an additional sclerite (Figs. 148–150), unlike *Leucauge*, *Meta* and *Metellina*.

Trichobothria are absent from the femur; there are two rows of dorsal trichobothria on basal third of tibiae, and there is one trichobothrium dorsally on proximal end of metatarsus.

Males slightly smaller than females, having elongate palpal articles and a spur distally on the long palpal trochanter (Figs. 145, 151). Males do not have coxae or legs modified.

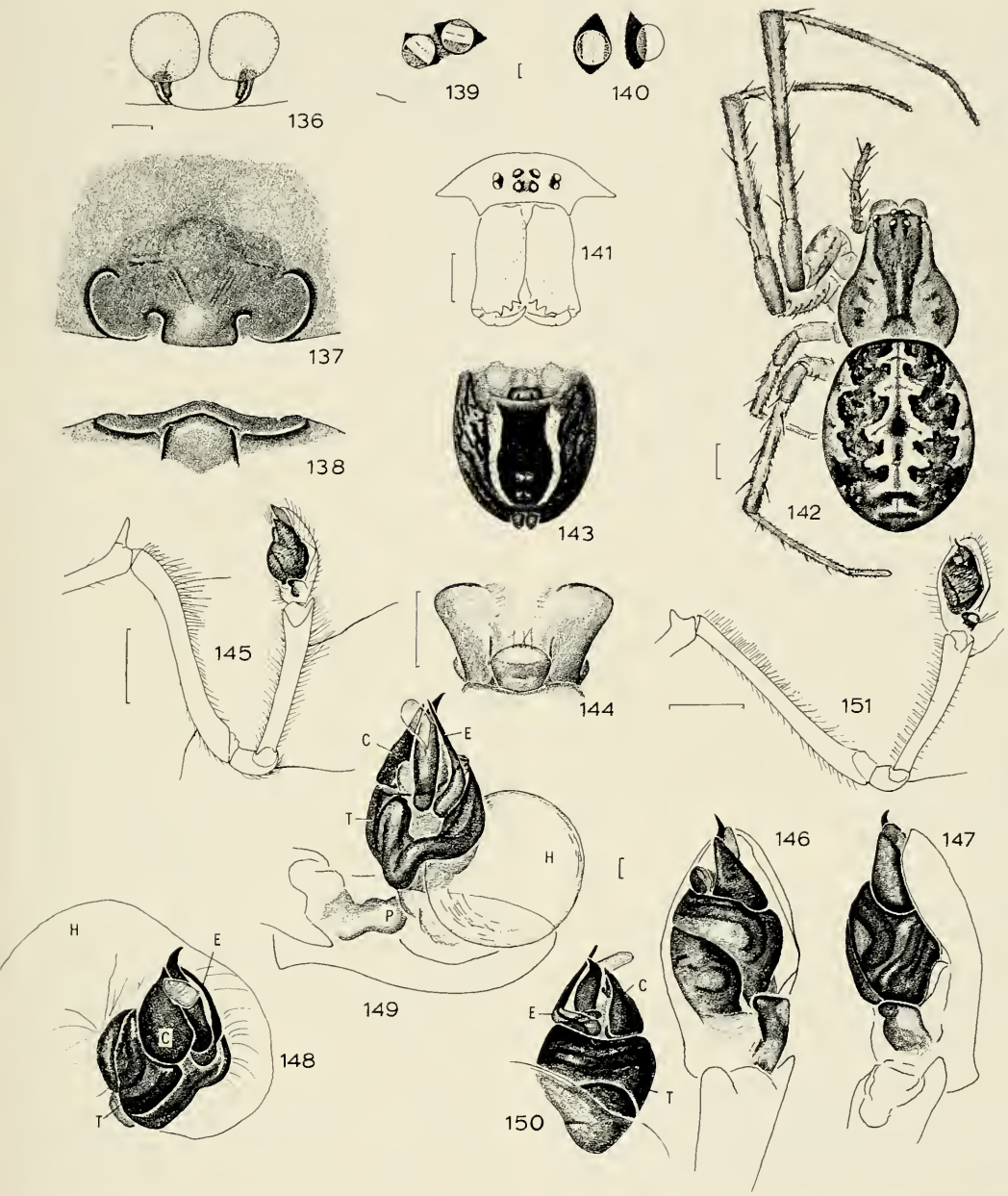


Map 6. Distribution of *Metleucauge eldorado* new species.

Genitalia. The epigynum is a sclerotized plate with the openings in slits on each side on the venter leading into lightly sclerotized seminal receptacles (Figs. 136–138). Again, I am uncertain if there are separate fertilization ducts, but I think these are present (Fig. 136).

The palpus differs from that of *Meta* or *Metellina* in having a much smaller paracymbium (P in Figs. 146, 147, 149), in having the duct in the tegulum (T) coiled as in *Leucauge*, and in having the conductor or embolus base broken, forming an additional sclerite (Figs. 148–150). The homology of this sclerite is not certain.

Description. Carapace brown, thorax light on each side, rim of thorax and thoracic depression darkest (Fig. 142). Chelicerae brown. Sternum dark. Coxae



Figures 136–150. *Metleucauge eldorado* new species. 136–144. Female. 136–138. Epigynum. 136. Dorsal, cleared. 137. Ventral. 138. Posterior. 139. Left lateral eyes. 140. Posterior median eyes. 141. Eye region and chelicerae. 142. Dorsal. 143. Ventral. 144. Labium and endites. 145–150. Left male palpus. 145. Ventrolateral. 146. Ventral. 147. Lateral. 148–150. Expanded. 148. Ventrolateral. 149. Dorsal. 150. Mesal.

Figure 151. *M. kompirensis* (Bösenberg and Strand), new combination, left palpus, subventral (Japan).

Scale lines. 0.1 mm; Figures 141–145, 151, 1.0 mm.

Abbreviations. C, conductor (uncertain); E, embolus; H, hematodocha; P, paracymbium.

light; distal articles of legs brown, fairly distinctly banded. Dorsum of abdomen variable with folium (Fig. 142), venter black with 2 white curved subparallel marks (Fig. 143).

Carapace narrow in front; eyes placed close together. Height of clypeus ranges from slightly less than one diameter to 1.5 diameters of anterior median eye. Anterior median eyes their diameter apart, two from laterals. Posterior median eyes 1.3 diameters apart, 1.5 from laterals. Secondary eyes with canoe tapetum (Figs. 139, 140). Chelicerae with three large teeth on anterior margin (Fig. 141), four on posterior. Endites much wider distally than proximally (Fig. 144). Abdomen longer than wide, widest in middle or anterior of middle (Figs. 142, 143).

Species. Only one species, *M. eldorado*, is found in North America, in California. Several very similar related species are found in the Far East: *M. yunohamensis* (Bösenberg and Strand) and *M. kompirensis* (Bösenberg and Strand) (Fig. 151) of Japan. Yaginuma (1958) already pointed out that the two Japanese species are quite different from the European *Meta* and ought to be placed in a separate genus.

Metleucauge eldorado new species
Figures 136–150; Map 6

Holotype. Female from rock on river bank, Sequoia National Park, Tulare County, California, 20 July 1968 (P. Nelson) in the Museum of Comparative Zoology.

Description. Female from King's Canyon, California. Carapace yellow-brown with median dark, tapering, longitudinal band, as wide as eye region in front and enclosing a light streak (Fig. 142). Margin of thorax with a narrow line; on side of thorax a dark "W," light towards median, fading into sides. Dark carapace areas with setae. Dark rings around eyes. Clypeus light. Chelicerae, endites, labium brown. Sternum dark, lightest in center. Legs banded. Dorsum of abdomen with branching, light cardiac mark. Posterior with light transverse marks. Sides of cardiac mark dark, these dark areas with light borders on sides (Fig. 142). Venter of abdomen black with two silvery longitudinal lines. Secondary eyes slightly smaller than anterior medians. Laterals on tubercles. Anterior median eyes their diameter apart, about 1.2 diameters from laterals. Posterior median eyes about 1.5 diameters apart, 1.5 diameters from laterals. The height of the clypeus is less than the diameter of the anterior median eyes. The chelicerae have three teeth on the anterior margin (Fig. 141), four on the posterior. The abdomen is oval, tapering to a point (Figs. 142, 143). Total length, 9.4 mm. Carapace, 4.5 mm long, 3.7 mm wide. First femur, 7.0 mm; patella and tibia, 8.9 mm; metatarsus, 7.6 mm; tarsus, 2.4 mm. Second patella and tibia, 6.6 mm; third, 3.8 mm; fourth, 5.5 mm.

Male. Male is darker than female. Thoracic depression like female, with two depressions side by side. Anterior lateral eyes subequal to anterior medians; posterior eyes slightly smaller. Chelicerae and endites slightly enlarged. Chelicerae with three teeth on anterior margin, three on posterior. Trochanter of palpus with spur (Fig. 145); palpal patella and tibia with one macroseta. Both articles elongated. Total length, 9.0 mm. Carapace, 4.7 mm long, 3.5 mm wide. First femur, 7.6 mm; patella and tibia, 9.4 mm; metatarsus, 8.4 mm; tarsus, 2.7 mm. Second patella and tibia, 7.2 mm; third, 3.6 mm; fourth, 5.4 mm.

Variation. Female 8.8 to 11.3 mm total length; carapace, 3.9 to 5.2 mm long, 3.3 to 4.2 mm wide. First patella and tibia, 7.6 to 9.6 mm long. Male 7.8 to 11.7 mm total length; carapace, 3.9 to 6.2 mm long, 3.1 to 4.8 mm wide; first patella and tibia, 9.2 to 11.5 mm long.

Diagnosis. The shape of the epigynum (Fig. 137), the shape of the sclerites in the palpus (Figs. 146, 147) and the shape of the trochanter tooth (Fig. 145) distinguish the species from the Asian *Metleucauge.*

Natural History. Males are almost as common in collections as females. All adults have been collected in July and August. The species makes an orb about 28 cm in diameter between rocks near streams.

Distribution. California.

Records. Paratypes. California. Eldorado Co.: W. of Kyburz, 3 July 1978, ♀ (D. Boe, MCZ). Glenn Co.: Brittan Ranch, 18 May 1968, ♂ (R. Hansen, CAS). Humboldt Co.: 10 mi E Bridgeville, 20 Aug. 1959, ♂ (V. Roth, W. J. Gertsch, AMNH); 2 mi S Blocksburg, stream under Alderpoint, 19 July 1968, 1♀ (H. B. Leech, CAS); 2 mi SE Hoopa, 23 Aug. 1969, 1♂ (M. M. Bentzien, EMUC). Kings Canyon Natl. Park: Cedar Grove, 16 July 1952, ♀ (W. J. Gertsch, AMNH); 5 July 1956, ♀, ♂ (V. Roth, W. J. Gertsch, AMNH); Sequoia Natl. Park: 3 mi W Giant Forest, 9 July 1958, ♀ (V. Roth, W. J. Gertsch, AMNH). Shasta Co.: Hatchet Creek, 10 mi W Burney, 1 Aug. 1953, ♀ (W. J. and J. W. Gertsch, AMNH); Hazel Creek, 4 July 1952, ♀ (W. J. Gertsch, AMNH). Sierra Co.: The Cups, Sierra City, 6 Sept. 1959, ♀, ♂ (V. Roth and W. J. Gertsch, AMNH). Siskiyou Co.: Ney Springs, 5 mi W Mt. Shasta, 2 Sept. 1959, ♂ (V. Roth and W. J. Gertsch, AMNH). Tulare Co.: Soda Creek, W of Nelson's Camp, 11 July 1958, ♀, ♂ (V. Roth and W. J. Gertsch, AMNH); McIntire Creek near Camp Nelson, 11 July 1958, ♀ (V. Roth and W. J. Gertsch, AMNH).

Tetragnathinae Menge, 1866
Pachygnatha Sundevall

Pachygnatha Sundevall, 1823, Specimen Academium Geneva Araneidum p. 16. Type species *P. clercki* by monotypy. The name is feminine.

Diagnosis. Pachygnatha differs from the *Meta* group of genera in lacking tapetum in the posterior median eyes, and in having the rhabdoms arranged in rows which loop (Figs. 157, 159, 161). Unlike *Tetragnatha*, the lateral eyes still have the canoe tapetum (Figs. 156, 158, 160). *Glenognatha* has similar eyes but has the ventral median spiracle moved anteriorly. *Pachygnatha* differs from *Tetragnatha* in having the abdomen ovoid to spherical (Figs. 171, 184, 244), and differs from all similar genera in having the sternum surround the coxae (Fig. 152). Unlike most Araneinae and Metinae, the height of the clypeus is equal to 2 diameters of the anterior median eyes (Figs. 154, 155, 162, 163). Like *Tetragnatha* and *Glenognatha*, female *Pachygnatha* lack an epigynum (copulatory pores).

Description. Carapace with median longitudinal dark band, and a band from thoracic depression anteriolateral between thorax and head (Figs. 171, 184, 196, 208, 232, 244). Indistinct dark patch on each side of thorax. Chelicerae and sternum orange to brown; coxae and legs much lighter, light yellow to orange, not banded. Abdomen dorsum with a folium bordered by dark marks with adjacent silver spots, folium usually with lobes posteriorly. Cardiac mark sometimes outlined by dark pigment, or with a median dark mark; often with paired white spots (Figs. 171, 184, 196, 208, 232, 244). Sides streaked; venter indistinctly marked (Fig. 172), sometimes having two fine longitudinal lines of white pigment spots which bend anteriorly and pass the booklung spiracles laterally (Fig. 185); usually with indistinct dark lines behind genital opening and dark pigment above genital area (Figs. 172, 209, 221, 233, 245). Carapace smooth without setae, but sometimes with indistinct punctate sculpturing. Head region set off by a depression on each side in groove between thorax and head (Figs. 171, 208, 244). Eyes closely grouped, median eyes their diameter apart, 1.5 to 2 diameters from laterals. Height of clypeus 2 to 3 diameters of anterior median eyes. Chelicerae very large and heavy, always with 3 teeth on anterior margin in female, usually 4 on posterior (3 in *P. autumnalis*) (Figs. 154, 155, 162). Those of male modified and expanded, sometimes with a spur outside, above base of fang (Figs. 215,

227). Southern females of *P. furcillata* also have a spur in this location (Fig. 165). Labium large, endites very long (Fig. 153), and sternum surrounding coxae varies (Fig. 152) slightly in different species. Sternum may be truncate or notched between posterior coxae (Fig. 152). All legs rather thin and lacking macrosetae, but with several trichobothria on femur at base; dorsally, several on tibia and usually one on metatarsus (Fig. 173). Abdomen subspherical, slightly flattened dorsoventrally (Figs. 171, 184). Book-lung spiracles rebordered, posterior median spiracle close to spinnerets (Figs. 168, 172, 217, 221).

Males are the same size as females, unlike most araneid spiders. The chelicerae are often enlarged and bent (Figs. 163, 203, 239).

Genitalia. The palpus is very simple but can be derived from a *Meta*- and *Leucauge*-like structure. There is a spherical tegulum (T in Fig. 177); from its tip there is only a long embolus (E) supported by a conductor (C). The cymbium (Y) is much modified and narrow, and the paracymbium (P in Fig. 177) is a free sclerite.

The female genitalia can easily be derived from the simple epigynum of *Meta*. A ventral lobe overhangs the original openings; a new median opening is posterior and separate from the book-lung spiracle. This leads into a chamber whose dorsal roof is a continuation of the ventral body wall, with continuous setation (Figs. 169, 170, 182, 183). Anterior of this new chamber is a second (perhaps the original) opening on each side leading into the very short connecting duct to a seminal receptacle. This in turn apparently leads into a very short fertilization duct to the anterior median chamber. The median chamber appears open toward the posterior. *Pachygnatha tristriata* appears to lack seminal receptacles (Figs. 242, 243). The use of only one palpus in mating (Gerhardt, 1921) rather than both simultaneously, as in haplogyne spiders, is further evidence that the epigynum is secondarily lost.

Species. Pachygnatha species are found in Eurasia, Africa and North America. None are known from the American tropics. There are eight species in North America, one of which is shared with Eurasia. Many European species have been illustrated by Wiehle (1963), others from the Iberian peninsula by Senglet (1972).

Diagnostic Species Characters. The males of each species are best separated by the palpi. The shape of the conductor and embolus and the paracymbium are diagnostic in ventral view (Figs. 176, 237, 249), but the paracymbium shows more variation than the embolus tip. Chelicerae modifications are variable and, although useful, are not the best diagnostic characters (Figs. 162–167).

Females may be difficult to separate. Chelicerae show considerable variation, but are always more elaborate in *P. furcillata*; southern *furcillata* females even have a spur on the anterior face above the base of the fang (Fig. 165). Trichobothria are present or sometimes absent on metatarsus (Figs. 173, 210, 222). Since their

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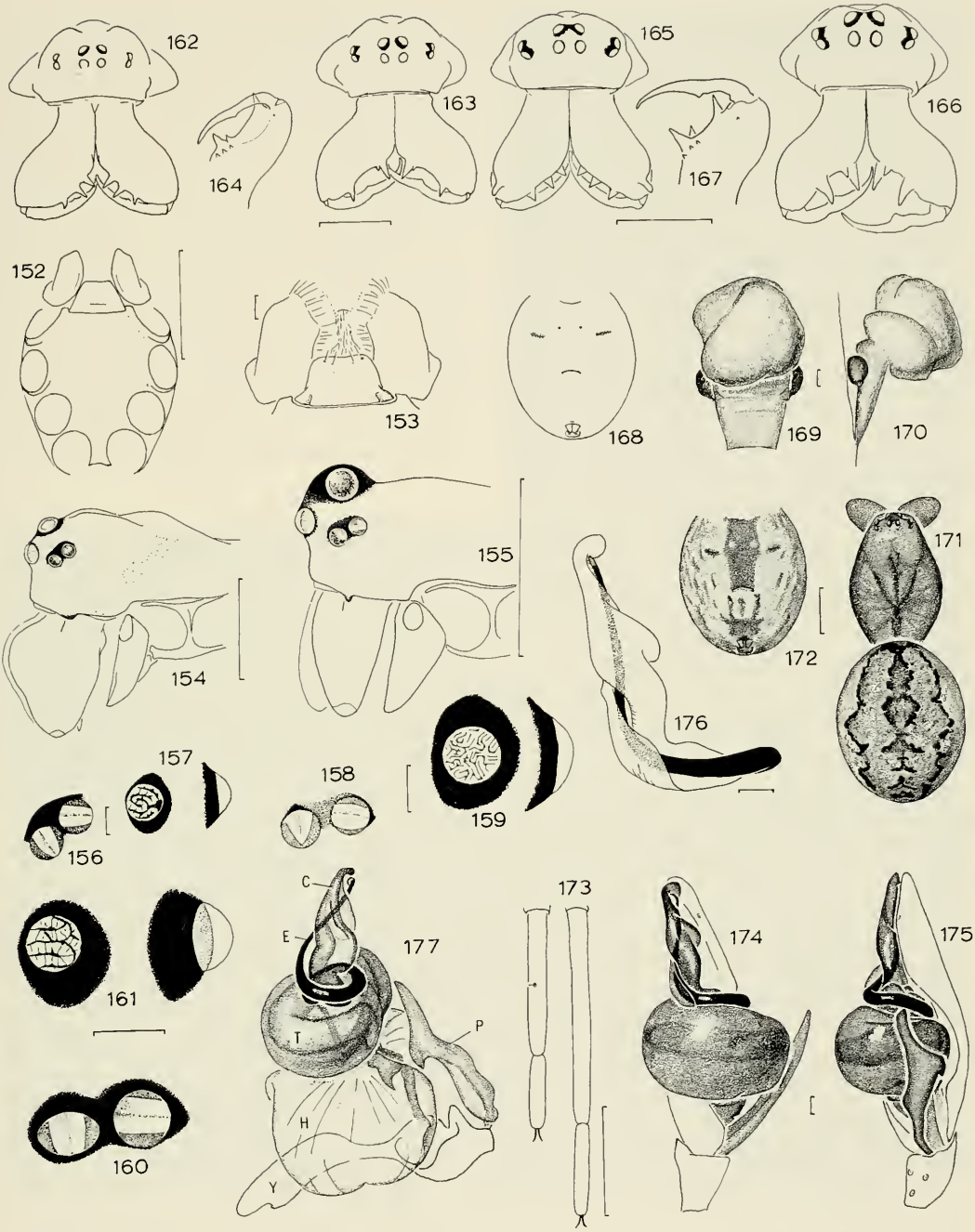
Figures 152–161. Morphology of *Pachygnatha*. 152. Sternum of *P. autumnalis*. 153. Labium and endites of *P. autumnalis*. 154, 155. Head and chelicerae. 154. *P. furcillata*. 155. *P. autumnalis*. 156–161. Secondary eyes. 156, 158, 160. Left laterals. 157, 159, 161. Posterior medians. 156, 157. *P. furcillata*. 158, 159. *P. autumnalis*. 160, 161. *P. xanthostoma*.

Figures 162–177. *P. furcillata* Keyserling. 162, 163, 165, 166. Eye region and chelicerae; 164, 167. Left chelicera, posterior view. 162, 165. Female. 163, 164, 166, 167. Male. 162–164. (Central New York State). 165–167. (Florida). 168–173. Female. 168. Position of genital opening. 169, 170. Internal genitalia. 169. Dorsal. 170. Lateral. 171. Dorsal. 172. Abdomen, ventral. 173. Left third and fourth metatarsus, dorsal. 174–177. Left male palpus; 174. Ventral. 175. Lateral. 176. Embolus and conductor, ventral. 177. Expanded, subventral.

Scale lines. 0.1 mm; Figures 152, 154, 155, 162–168, 171–173, 1.0 mm.

Abbreviations. C, conductor; E, embolus; H, hematodocha; P, paracymbium; Y, cymbium.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hairs are short, they are not as easy to find as in other groups; those of the metatarsus are easiest to locate. The placement of the trichobothria is not as constant as might be expected; that of the third metatarsus of *P. furcillata* may be in the middle of the article or closer to the proximal end. The placement was first carefully measured, but was found too variable to use as diagnostic character.

It is of interest that the two specialized *Pachygnatha*, *P. autumnalis* and *P. tristriata* (judged by the shape of the carapace and by the unusual structure of the male palpus), also have the trichobothrium distally on the metatarsus, a unique position in the superfamily. The trichobothrium is usually found proximally on the metatarsus in Araneoidea.

The seminal receptacles are of a distinct shape in *P. autumnalis* (Fig. 207), and the anterior soft parts appear diagnostic (Figs. 169, 170, 182, 183, 194, 195). The genital opening may be in the middle of the abdomen (Fig. 193), while in others of the same species more anterior, depending on the fullness of the abdomen. The width of the opening appears diagnostic, as well as its distance from an imaginary line between the book-lung spiracles or from the two small muscle sclerites between the spiracles (Figs. 181, 193).

Natural History. All *Pachygnatha* species are found in moist places on the ground (Plate 7); adults have lost the ability to make webs. *Pachygnatha* adults have reduced accessory claws needed for handling silk. I have examined the leg tips of a less than half-grown *P. autumnalis* and found the accessory claws present but almost smooth, appearing like other setae. Wiehle (1963) cites Apstein, observing that *Pachygnatha* lacks aggregate glands, which produce the viscid droplets on silk.

Balogh (1934) observed young to make webs. Wiehle (1963) questioned this observation and cites Homann raising *Pachygnatha* to the third molt without seeing webs. Balogh promised a further description of the web, but this was never published. Martin (1978) again reports finding the web of young *Pachygnatha* (1.3 to 1.8 mm total length) in Germany. The diameter is 4 to 6 cm; there are 13 to 17 radii, and an open hub. It is built horizontally between plants, at a height of 2 to 8 cm. The web is fine and hard to see. Young *Pachygnatha* have more distinct accessory claws than adults, and possess aggregate and flagelliform glands like other ecribellate orb-weavers. Martin's specimens examined by Thaler and Homann (personal communication) were found to lack tapetum in the posterior median eyes, thus undoubtedly belonging to *Pachygnatha*, probably *P. degeeri*.

KEY TO FEMALE *PACHYGNATHA*

1. Posterior median eyes 2 to 3 times diameter of posterior laterals (Figs. 155, 202); only 3 teeth on posterior margin of chelicerae ---- *autumnalis*
– Posterior median eyes 1 to 1.5 times diameter of posterior laterals (Figs. 154, 214); 4 teeth on posterior margin of chelicerae ---- 2
2(1). Genital area covered by a thin, triangular sclerite longer than wide (Fig. 241, 245); dorsum of abdomen with two curved longitudinal lines, not wavy behind (Fig. 244) ---- *tristriata*
– Genital area without such sclerite (Figs. 229, 233); dorsal abdominal lines wavy behind or broken (Fig. 232) ---- 3
3(2). Total length less than 4.2 mm ---- *xanthostoma*
– Total length more than 4.5 mm ---- 4
4(3). Trichobothrium dorsally on fourth metatarsus (Fig. 234); Alaska, Canada ---- *clercki*
– Fourth metatarsus never with trichobothrium (Fig. 173) ---- 5
5(4). Head with bulge on each side (Figs. 154, 162, 165); chelicerae elongated and curved (Figs. 162, 165); trichobothrium on third metatarsus dorsal and near middle of article (Fig. 173) ---- *furcillata*
– Head without bulges (Figs. 178, 190); chelicerae fairly straight (Figs. 178, 190); third metatarsus trichobothrium posterodorsal, twice as far from distal end of article as from proximal end (Figs. 186, 198) ---- 6
6(5). Genital opening one to 1½ times its width distant from two tiny sclerites between book-lung spiracles (Fig. 181); in middle or closer to sclerites between book-lungs than to spinnerets (Fig. 181) ---- *brevis*

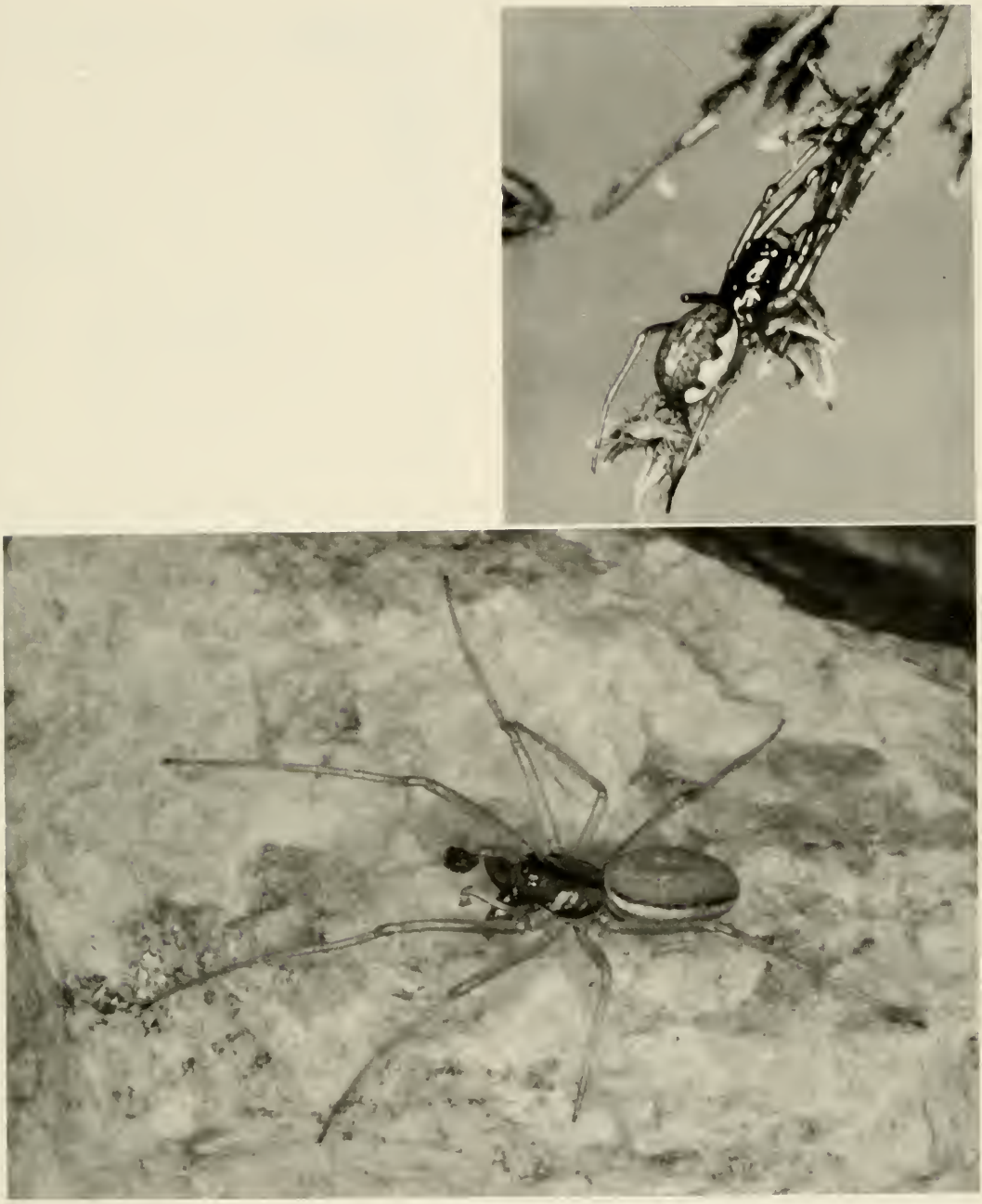
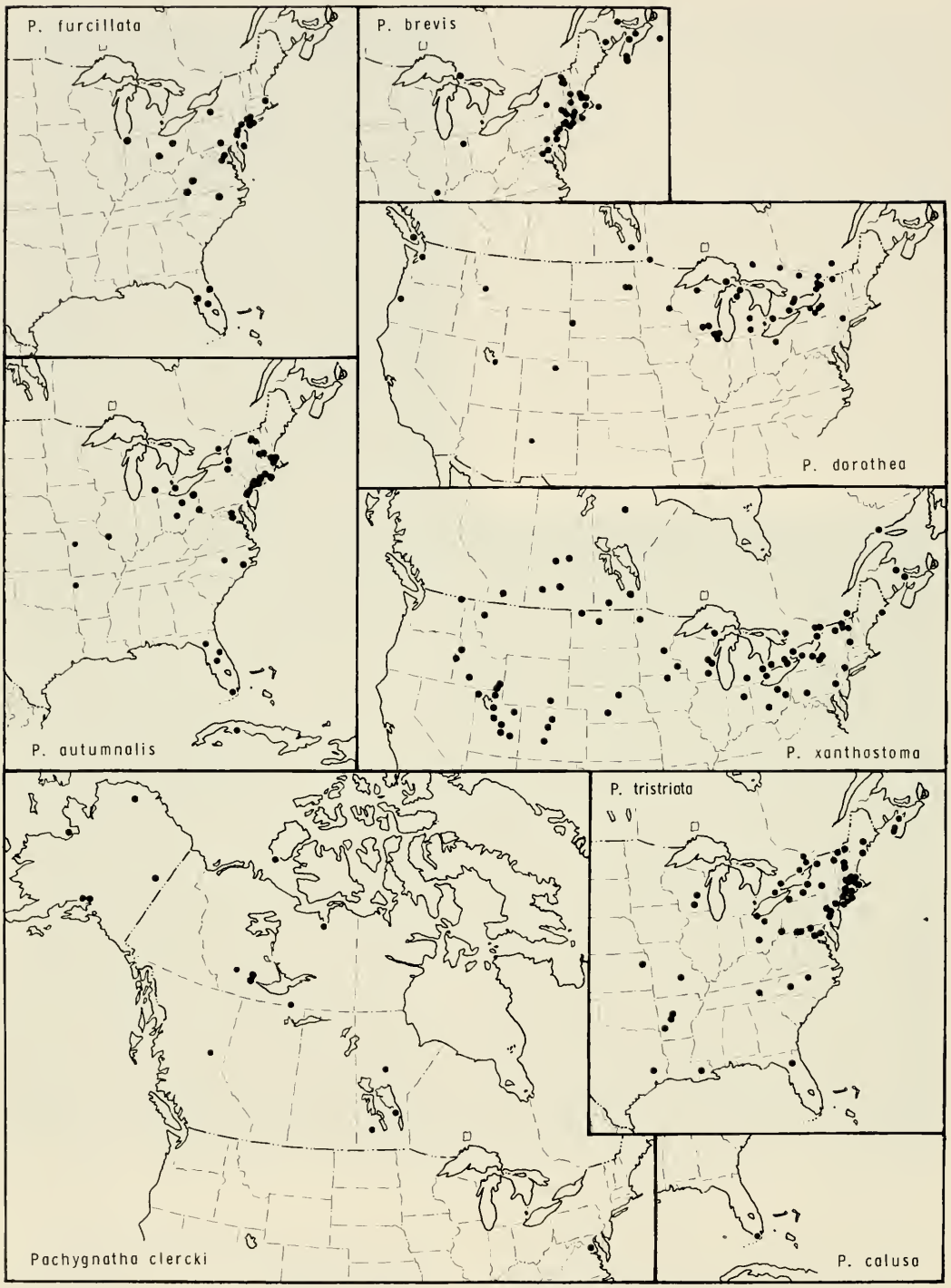


Plate 7. Above, *Pachygnatha autumnalis* Keyserling, female; below, *P. tristriata* C. L. Koch, male.

– Genital opening two or more times its width distant from two tiny sclerites between book-lung spiracles (Fig. 193); closer to spinnerets than to book-lungs (Fig. 193) ..... *dorothea*

Key to Male *Pachygnatha*

1. Spur on outside of chelicerae above base of fang (Figs. 215, 227) 2
– Chelicerae without such spur (Figs. 166, 203, 239) 4



Map 7. Distribution of *Pachygnatha* species.

2(1). Embolus and conductor length 2 to 3 times length of spherical tegulum (Fig. 223) ..... *xanthostoma*

– Embolus and conductor at most 1.5 times length of tegulum (Fig. 235) 3

3(2). Duct in tegulum undulating (Fig. 235); paracymbium distally entire (Fig. 236); total length more than 4.0 mm; Alaska, Canada ..... *clercki*

– Duct in tegulum straight (Fig. 252); paracymbium distally with a notch (Fig. 253); total length less than 2.0 mm; Florida ..... *calusa*

4(1). Posterior median eyes two to three times diameter of posterior laterals (Fig. 203); conductor pointed away from cymbium, notched at tip (Fig. 213); paracymbium straight and pointed (Fig. 212) .. *autumnalis*

– Posterior median eyes one and one-half times diameter to subequal of posterior laterals (Fig. 215); conductor not notched at tip (Figs. 176, 189, 201); tip of paracymbium curved (Figs. 175, 188, 200) 5

5(4). Conductor straight, embolus coiled behind tegulum; length of conductor and embolus two to three times length of spherical tegulum (Fig. 247); abdomen with 2 curved longitudinal lines not wavy behind (Fig. 244) ..... *tristriata*

– Conductor lobed or twisted, embolus not coiled behind tegulum; length of conductor and embolus less than twice length of spherical tegulum (Figs. 187, 199); two broken lines on dorsum of abdomen waving toward posterior (Figs. 184, 196) 6

6(5). Distal part of paracymbium without neck, tip pointed toward cymbium (Fig. 175); head with swelling on each side (Figs. 154, 163, 166) ..... *furcillata*

– Distal part of paracymbium with narrow neck, tip pointed away from cymbium (Figs. 188, 200); head without swelling (Fig. 184, 196) 7

7(6). In ventral view of palpus, base of conductor not visible above wide embolus (Fig. 189) ..... *brevis*

– In ventral view of palpus, base of conductor visible above embolus (Fig. 201) .. *dorothea*

Pachygnatha furcillata Keyserling
Figures 154, 156, 157, 162–176; Map 7

Pachygnatha furcillata Keyserling, 1884, Verhandl. Zool. Bot. Ges. Wien, 32: 662, pl. 21, fig. 11, ♀. Female syntypes from Philadelphia in the Marx collection of the U.S. National Museum of Natural History, lost; one female in the Keyserling collection of the British Museum, Natural History, examined. McCook, 1894, American Spiders, 3: 271, pl. 28, fig. 3, ♀. Bryant, 1933, Bull. Mus. Comp. Zool., 74: 177, pl. 4, figs. 38, 39, ♂. Kaston, 1948, Bull. Connecticut Geol. Natur. Hist. Surv., 70: 267, figs. 842, 858, ♀, ♂.

Description. Female. Carapace orange with darker lines. Head and eye area yellow. Chelicerae yellow-orange. Dorsum of folium with angular lobes posteriorly (Fig. 171). Head with a bulge on each side (Figs. 154, 162, 165, 171); in dorsal view, head outline not constricted behind (Fig. 171). The genital opening is narrow, a distance of about twice its width from the two muscle sclerites between the book-lungs (Fig. 168), closer to book-lungs than to spinnerets. Trichobothrium on middle of third metatarsus, none on fourth metatarsus (Fig. 173). Total length, 6.6 mm. Carapace, 3.2 mm long, 2.2 mm wide. First femur, 3.2 mm long; patella and tibia, 4.0 mm; metatarsus, 2.7 mm; tarsus, 1.4 mm. Second patella and tibia, 3.5 mm; third, 2.2 mm; fourth, 3.0 mm.

Male. Three posterior cheliceral teeth closely spaced, one close to base of fang (Fig. 167). Total length, 5.5 mm. Carapace, 2.7 mm long, 2.0 mm wide. First femur, 3.3 mm; patella and tibia, 4.1 mm; metatarsus, 2.7 mm; tarsus, 1.4 mm. Second patella and tibia, 3.7 mm; third, 2.2 mm; fourth, 3.2 mm.

Variation. Female total length, 5.2 to 6.2 mm; carapace, 2.4 to 2.9 mm long. Male total length, 4.6 to 5.9 mm; carapace, 2.3 to 2.9 mm long. The smallest specimens come from the southeastern states. Adult and juvenile females from the southeastern states may have a spur above the fang base on the chelicerae (Fig. 165); the fang is minute in some, absent in northern specimens. (The eyes appear larger in Fig. 165 than in Fig. 162 because of the size difference: the smaller southern specimen has relatively larger eyes.)

Diagnosis. Females of this species are readily identified by their light head with bulges on each side (Figs. 154, 162, 171). Females from the southeastern states may have a spur on the chelicerae

above the base of the fang (Fig. 165). Males are identified by the knobbed tip and lateral lobe on the tip of conductor (Figs. 174, 176) and by the tip of the paracymbium pointed toward the cymbium (Fig. 175).

Natural History. The species has been collected from a cedar bog in Ohio, a bog in Massachusetts, bottom land hardwood in North Carolina.

Distribution. New England west to Indiana, south to Florida (Map 7).

Pachygnatha brevis Keyserling
Figures 178–189; Map 7

Pachygnatha tristriata:—Keyserling, 1882, Verhandl. Zool. Bot. Ges. Wien, 32: 209 (not *P. tristriata* C. L. Koch).

P. brevis Keyserling, 1883, Verhandl. Zool. Bot. Ges. Wien, 33: 658. New name for *P. tristriata*:—Keyserling, 1882, misidentified. Male specimen marked "Amer. N." in the Muséum National d'Histoire Naturelle, Paris, examined and labeled lectotype. Emerton, 1884, Trans. Connecticut Acad. Sci., 6: 336, pl. 34, fig. 21, pl. 40, figs. 8, 10, ♀, ♂. ?McCook, 1894, American Spiders, 3: 267, pl. 26, figs. 9, 10a, pl. 28, fig. 2, ♀, ♂. Comstock, 1912, *The Spider Book*, p. 407, figs. 101, 418, ♂. Kaston, 1948, Bull. Connecticut Geol. Natur. Hist. Surv., 70: 267, figs. 841, 857, ♀, ♂.

Note. A collection labeled in pencil *Pachygnatha tristriata* C. L. Koch, Amer. N., no. 2942 was found within the collection of the Paris museum. In the vial was one shriveled *P. tristriata* female, two male *P. clercki*, and one pair of *P. brevis*. The male of the two was marked lectotype, the female, paralectotype.

Description. Female. Carapace with dark band enclosing median eyes (Fig. 184). Dorsum of folium lobed in posterior part (Fig. 184). Carapace has a constriction between head and thorax (Fig. 184) in dorsal view. The genital opening is a distance about equal to its width or one and one-half times its width from the two sclerites between the book-lungs; it is equidistant or closer to sclerites than to spinnerets (Fig. 181). Third metatarsus has a trichobothrium one third distance from proximal end in slightly posterior position; the fourth lacks a trichobothrium (Fig. 186). Total length, 5.6 mm. Carapace, 2.7 mm long, 1.9 mm wide. First femur, 2.7 mm; patella and tibia, 3.5 mm; metatarsus, 2.3 mm; tarsus, 1.2 mm. Second patella and tibia, 3.2 mm; third, 1.9 mm; fourth, 2.7 mm.

Male. Posterior of the chelicerae with four teeth, the distal three almost equally spaced (Fig. 180). Total length, 5.5 mm. Carapace, 2.7 mm long, 2.0 mm wide. First femur, 2.8 mm; patella and tibia, 3.6 mm; metatarsus, 2.4 mm; tarsus, 1.2 mm. Second patella and tibia, 3.5 mm; third, 2.0 mm; fourth, 2.7 mm.

Variation. Female total length 4.6 to 5.5 mm; carapace 2.4 to 2.6 mm long. Male total length 4.5 to 5.6 mm; carapace 2.2 to 2.6 mm long.

Diagnosis. This species is easily confused with *P. dorothea*; females are difficult to separate. The females can be distinguished by the wide genital opening, equidistant from spinnerets and book-lungs or closer to book-lungs (Fig. 181). The male can be separated from *P. dorothea* by the heavy embolus (Fig. 189).

Natural History. Specimens have been collected from swamps in New England, salt marsh in Maryland, and in an asparagus bed in Massachusetts.

Distribution. Nova Scotia, New En-

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Figures 178–189. *Pachygnatha brevis* Keyserling. 178–180. Eye region and chelicerae. 178. Female. 179, 180. Male. 180. Left chelicera, posterior. 181–186. Female. 181. Position of genital opening. 182, 183. Female genitalia. 182. Dorsal. 183. Lateral. 184. Dorsal. 185. Abdomen, ventral. 186. Third metatarsus and tarsus, dorsal. 187–189. Left male palpus. 187. Ventral. 188. Lateral. 189. Embolus and conductor, ventral (embolus black).

Figures 190–201. *P. dorothea* McCook. 190–192. Eye region and chelicerae. 190. Female. 191, 192. Male. 192. Left chelicera, posterior. 193–198. Female; 193. Position of genital opening. 194, 195. Female genitalia. 194. Dorsal. 195. Lateral. 196. Dorsal. 197. Abdomen, ventral. 198. Third metatarsus and tarsus, dorsal. 199–201. Male palpus. 199. Ventral. 200. Lateral. 201. Embolus and conductor, ventral.

Scale lines. 0.1 mm; Figures 178–181, 184–186, 190–193, 196–198, 1.0 mm.

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gland to Virginia west to Indiana (Map 7). The westernmost localities are Fort Wayne, Indiana, ♀, ♂, 3 Aug. 1964 (W. Ivie) and Sable River, Ontario, ♂, Aug. 1963 (C. B. Powell).

Pachygnatha dorothea McCook
Figures 190–201; Map 7

Pachygnatha dorothea McCook, 1893, American Spiders, 3: 270, pl. 26, figs. 3, 4, ♀, ♂. Female and male syntypes from neighborhood of Philadelphia in the Academy of Natural Sciences, Philadelphia, lost. Male neotype here designated from Ithaca, New York (N. Banks) in the Museum of Comparative Zoology.

Pachygnatha kuratai Levi, 1951, Amer. Mus Novitates, 1501: 15, figs. 29–31, ♀, ♂. Male holotype from Toronto, Canada in the American Museum of Natural History, examined. NEW SYNONYMY

Note. McCook illustrated a right palpus, which shows by the base of the conductor that it is clearly this species. The new type locality is a place where this species is common and from which there are numerous collections.

Description. Female. Carapace orange with median longitudinal dark line enclosing median ocular quadrangle (Fig. 196). Dorsum of abdomen with dark spots on each side (Fig. 196). Genital opening is the distance of two to three times its width from the sclerites between the book-lung spiracles; it is closer to spinnerets than to book-lungs (Fig. 193). Trichobothrium of third metatarsus one third its length from proximal end (Fig. 198). Total length, 5.0 mm. Carapace, 2.4 mm long, 1.7 mm wide. First femur, 2.4 mm; patella and tibia, 3.2 mm; metatarsus, 2.0 mm; tarsus, 1.1 mm. Second patella and tibia, 3.0 mm; third, 1.8 mm; fourth, 2.6 mm.

Male. Chelicerae with four teeth on posterior margin in two groups of two (Fig. 192). Total length, 5.5 mm. Carapace, 2.4 mm long, 1.9 mm wide. First femur, 2.6 mm; patella and tibia, 3.5 mm; metatarsus, 2.2 mm; tarsus, 1.2 mm. Second patella and tibia, 3.2 mm; third, 2.0 mm; fourth, 2.4 mm.

Variation. Females, total length, 5.0 to 6.2 mm; carapace, 2.5 to 2.7 mm long. Males, total length, 4.7 to 6.0 mm; carapace, 2.3 to 2.7 mm long.

Diagnosis. The species has often been called *P. brevis*; the two are very similar and females are difficult to separate. The female can best be identified by the genital opening which is closer to the spinnerets than to the sclerites between the book-lung spiracles (Fig. 193). The genital opening is narrower than that of *P. brevis*. The males have a more slender conductor and embolus than that of *P. brevis*; in ventral view the base of the conductor is visible (Fig. 199, 201).

Natural History. This species has been collected from lake shores, river banks, flood plains; in skunk cabbage, pitcher plants, and under the bark of trees.

Knutson (1979) reports that 40 out of 150 skunk cabbage (*Symplocarpus foetidus*) flowers growing through a foot of snow in April in Michigan were occupied by one or more *P. brevis* [*P. dorothea, sic*]. There were no webs and none of the spiders was feeding, although there were insects on the warm plants that had melted their way through the snow.

Distribution. Quebec, Ontario, New York to British Columbia, south to Oregon and New Mexico (Map 7). The southernmost record is San Fidel, Valencia

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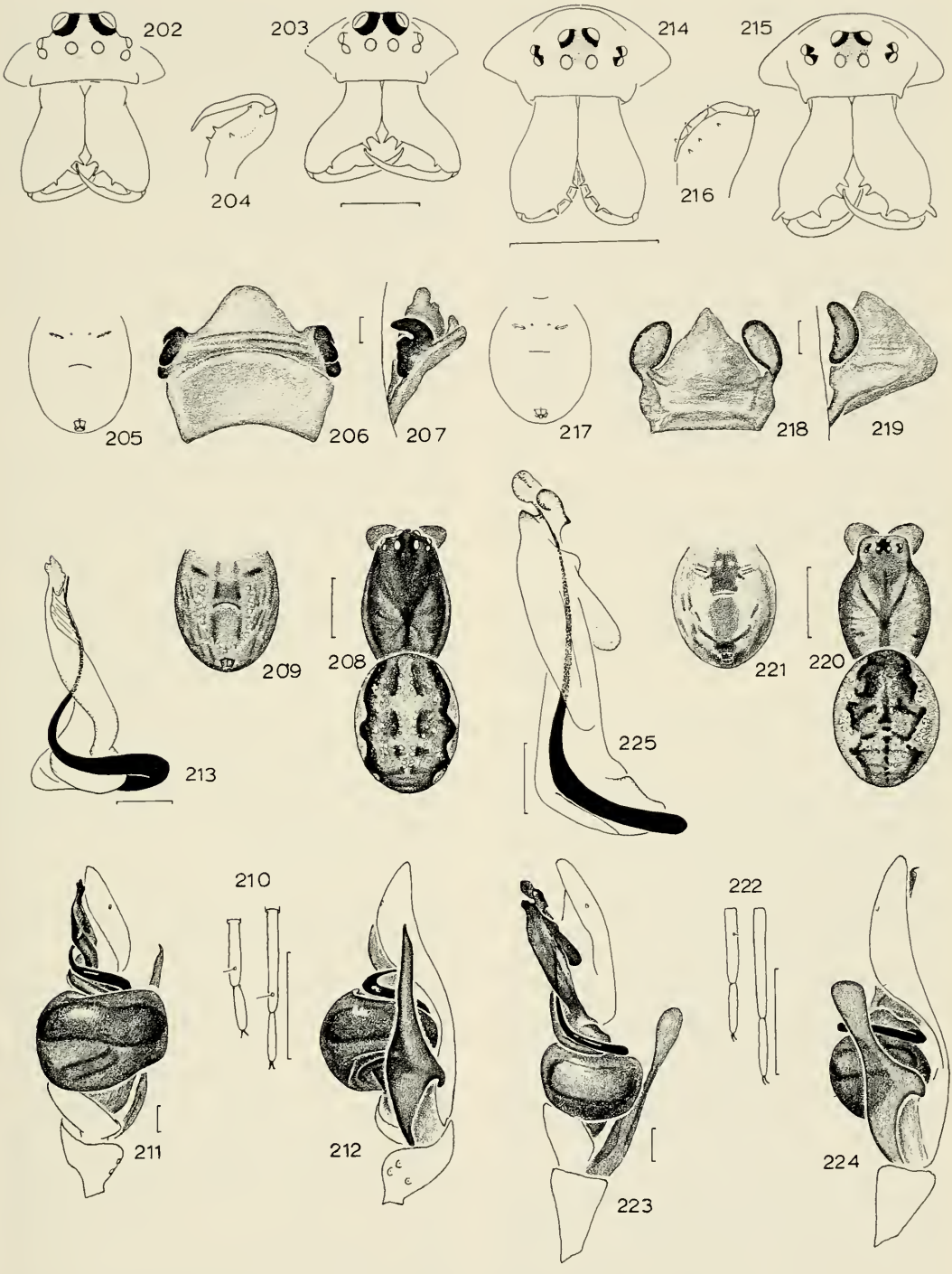
Figures 202–213. *Pachygnatha autumnalis* Keyserling. 202–204. Eye region and chelicerae. 202. Female. 203, 204. Male. 204. Left chelicera, posterior. 205–210. Female. 205. Position of genital opening. 206, 207. Female genitalia. 206. Dorsal. 207. Lateral. 208. Dorsal. 209. Abdomen, ventral. 210. Left third and fourth metatarsi, tarsi, dorsal. 211–213. Left male palpus. 211. Ventral. 212. Lateral. 213. Embolus and conductor, ventral.

Figures 214–225. *P. xanthostoma* C. L. Koch. 214–216. Eye region and chelicerae. 214. Female. 215, 216. Male. 216. Chelicera, posterior. 217–222. Female. 217. Position of genital opening. 218, 219. Female genitalia. 218. Dorsal. 219. Lateral. 220. Dorsal. 221. Abdomen, ventral. 222. Third and fourth metatarsi and tarsi, posterodorsal. 223–225. Male palpus. 223. Ventral. 224. Lateral. 225. Embolus and conductor, ventral.

Scale lines. 0.1 mm; Figures 202–205, 208–210, 214–217, 220–222, 1.0 mm.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Co., New Mexico, ♀, 4 Sept. 1941 (W. Ivie).

Pachygnatha autumnalis Keyserling
Plate 7; Figures 155, 158, 159, 202–213; Map 7

Pachygnatha autumnalis Keyserling, 1884, Verhandl. Zool. Bot. Gesell. Wien, 33: 660, pl. 21, fig. 10, ♂. Male holotype allegedly from Harrisburg, Pennsylvania in the Marx collection of the U.S. National Museum of Natural History on permanent loan to the American Museum of Natural History, examined. Emerton, 1884, Trans. Connecticut Acad. Sci., 6: 337, pl. 34, fig. 22, pl. 40, fig. 9, ♀, ♂. McCook, 1893, American Spiders, 3: 268, pl. 26, figs. 1, 2, ♀, ♂. Roewer, 1942, Katalog der Araneae, 1: 998. Kaston, 1948, Bull. Connecticut Geol. Natur. Hist. Surv., 70: 266, figs. 840, 849, ♀, ♂.

Description. Female. Carapace dark brown with a light patch on each side of thorax posteriorly and a light rim around thorax (Fig. 208). Folium very distinct and posteriorly lobed, cardiac mark reddish (Fig. 208). Head region of carapace not distinctly set off from thorax (Fig. 208). Eye area raised (Figs. 155, 202). Posterior median eyes 1.7 diameters of anterior medians. Laterals 0.8 diameters of anterior medians. Anterior medians their diameter apart, one diameter from laterals. Posterior median eyes their diameter apart, 0.8 diameters from laterals. The genital slit is about its width distant from the two sclerites between the lung slits (Fig. 205). Chelicerae with only three teeth, all small, on the posterior margin; two proximally and one near base of fang. Metatarsi 3 and 4 have a trichobothrium close to the distal end (Fig. 210). Total length, 4.7 mm. Carapace, 2.2 mm long, 1.6 mm wide. First femur, 2.0 mm; patella and tibia, 2.4 mm; metatarsus, 1.6 mm; tarsus, 1.0 mm. Second patella and tibia, 2.1 mm; third, 1.4 mm; fourth, 2.0 mm.

Male. Color like female. Chelicerae as figured. Total length, 4.3 mm. Carapace, 1.9 mm long, 1.3 mm wide. First femur, 1.9 mm; patella and tibia, 2.3 mm; metatarsus, 1.4 mm; tarsus, 0.8 mm. Second patella and tibia, 1.9 mm; third, 1.2 mm; fourth, 1.7 mm.

Variation. Female total length, 4.2 to 5.0 mm; carapace, 2.0 to 2.4 mm long. Male total length, 3.5 to 4.3 mm; carapace, 1.9 to 2.0 mm long.

Note. The large eyes have very small rhabdom cells (Fig. 159), the lines of Fig. 159 show the dark pigment between the rhabdom rows. The size is presumably a functional adaptation.

Diagnosis. This species can be readily separated from others by its relatively small size and the enormous posterior median eyes, which are raised above the carapace (Fig. 155, 208). Females have only 3 teeth on the posterior margin of the chelicerae; all other species have 4. Males can be distinguished by the presence of a twisted embolus and conductor of the palpus (Figs. 211, 213), and by a very long pointed paracymbium (Fig. 212). Females are distinguished by the very characteristic shape of the seminal receptacle in side view (Fig. 207).

Natural History. This species has been collected using pit-fall traps in low woods, flat pine land in Florida, and in old fields.

Distribution. Ontario, New England south to Cuba, west to Missouri and Arkansas (Map 7). The Cuban record is from Soledad near Cienfuegos, Valles, Cuba, ♀ (P. J. Darlington).

Pachygnatha xanthostoma C. L. Koch
Figures 160, 161, 214–225; Map 7

Pachygnatha xanthostoma C. L. Koch, 1845, Die Arachniden, 12: 148, figs. 1068, 1069, ♀, ♂. Original specimens from Pennsylvania lost (M. Moritz, pers. communication). Male neotype here designated from Horseshoe Bend, northeast of Jamison, Bucks County, Pennsylvania, 1959 (W. Ivie) in the American Museum of Natural History. Keyserling, 1884, Verhandl. Zool. Bot. Gesell. Wien, 33: 659, pl. 21, fig. 9, ♂. McCook, 1893, American Spiders, 3: 269, pl. 26, figs. 7, 8, ♀, ♂.

P. dorothea:—Bryant, 1933, Bull. Mus. Comp. Zool., 74: 176, figs. 37, 41, ♂ (misidentified, not *P. dorothea* McCook).

Note. The type of *P. xanthostoma* has been lost and there is no evidence that it ever was in the Berlin Museum (M. Moritz, letter). *Pachygnatha xanthostoma* came from Pennsylvania, was 2¼ lines long (4.8 mm, probably with chelicerae; Koch

had his specimens on pins). Koch described it as having a punctate sternum and a carapace in part similarly sculptured; "thorax wider than head, rounded, palpi and legs like *Pachygnatha degeeri* [the smallest European species], and the chelicerae and legs yellow." I consider this description most applicable to the species described below, although the head and chelicerae are often darker. The species described below is the most similar to the European *P. degeeri*, and the proportions of the palpi of the two are similar. It has the most sculptured carapace and sternum of the American species and is also the most common.

The first reviser of *Pachygnatha*, Keyserling, 1884, considered this species to be *xanthostoma* and illustrated the diagnostic chelicerae. In collections this species has been called *xanthostoma* on labels by Bishop, Crosby and Gertsch, before 1933. Miss Bryant, however, decided in 1933 that *xanthostoma* was an older name for *P. brevis* Keyserling. She indicated as evidence that in 1912 N. Banks examined the Koch types at the Berlin Museum and found that the species labeled *P. xanthostoma* was what had been called *P. brevis*. This is an error. Miss Bryant also confused two species under the name of *brevis*: *brevis* and *dorothea*.

Description. Female. Dorsum of abdomen with an indistinct, lobed folium enclosing a few white, paired spots and a cardiac mark, as well as a broken median, longitudinal line; it is dusky to black (Fig. 220). Punctate marks are visible on some areas of carapace and on sternum. The genital opening is one-third the distance from a line between book-lungs to spinnerets (Fig. 217). Third metatarsus has trichobothrium one third its distance from proximal end and no trichobothrium on fourth metatarsus (Fig. 222). Total length, 3.5 mm. Carapace, 1.7 mm long, 1.3 mm wide. First femur, 1.4 mm; patella and tibia, 1.9 mm; metatarsus, 1.3 mm; tarsus, 0.7 mm. Second patella and tibia, 1.7 mm; third, 1.2 mm; fourth, 1.6 mm.

Male. Total length, 3.3 mm. Carapace, 1.7 mm long, 1.2 mm wide. First femur, 1.5 mm; patella and tibia, 1.9 mm; metatarsus, 1.3 mm; tarsus, 0.7 mm. Second patella and tibia, 1.8 mm; third, 1.0 mm; fourth, 1.7 mm.

Variation. Female total length, 3.0 to 4.2 mm; carapace, 1.6 to 1.9 mm long. Male total length, 2.9 to 3.8 mm; carapace, 1.4 to 1.8 mm long.

Diagnosis. Females can be separated from most American species by the small size, from *P. autumnalis* by small posterior median eyes (Fig. 214) and by the presence of a trichobothrium on the proximal third of the third metatarsus, and by the absence of trichobothrium on the fourth metatarsus (Fig. 222). Males have a very small tegulum, a very long and complex conductor (Figs. 223, 225), and a knobbed paracymbium (Fig. 224). Except for *P. clercki* and *P. calusa* it is the only male with a spur on the chelicerae above the origin of the fang (Fig. 215).

Natural History. This species has been collected from pitfall traps, sifted leaves in Michigan, lawn in Wisconsin, under boards in Nebraska, in grass near a stream in Utah, under a post by a pond in a hay meadow in Colorado, in an alfalfa field in Wyoming, and in the stomach of a toad (*Bufo*) collected in Montana.

Distribution. Quebec to Alberta, northern New England to Pennsylvania, west to Washington, Idaho and Utah (Map 7).

Pachygnatha clercki Sundevall
Figures 226–237; Map 7

Pachygnatha clercki Sundevall, 1823, Specimen Academicum Geneva, Araneidum Sueciae Exhibens, p. 16. Specimens from Sweden. Roewer, 1942, Katalog der Araneae, 1: 996. Locket and Millidge, 1953, British Spiders, 2: 106, figs. 71, 72, 73A, D, ♀, ♂. Bonnet, 1958, Bibliographia Araneorum, 2: 3277. Wiehle, 1963, Tierwelt Deutschlands, part 49: 61, figs. 99–106, ♀, ♂.

Pachygnatha sewardi Chamberlin and Ivie, 1947, Bull. Univ. Utah, biol. ser., 10(3): 64, figs. 76–78, ♀, ♂. Male holotype from Beluga Flats, Cook Inlet, Alaska in the American Museum of Natural History, examined. NEW SYNONYMY.

Note. The illustrations were all made from North American specimens, the palpi were made from paratypes of *P. sewardi*.

Description. Female. Dorsum of abdomen with indistinct folium, only dark outline present; posteriorly the dark bands are broken, but are not wavy (Fig. 232). The sternum lacks connection between coxae 1 and 2 to the narrow dorsal plate above. The genital slit is only one-

fourth the distance from a line between book-lungs to the spinnerets (Fig. 229). One trichobothrium on middle of metatarsus 3, and one two-thirds the distance from proximal end on metatarsus 4 (Fig. 234). Total length, 5.5 mm. Carapace, 2.6 mm long, 1.9 mm wide. First femur, 2.5 mm; patella and tibia, 3.2 mm; metatarsus, 2.0 mm; tarsus, 1.2 mm. Second patella and tibia, 2.9 mm; third, 1.9 mm; fourth, 2.6 mm.

Male. Coloration more distinct than female. Total length, 5.3 mm. Carapace, 2.4 mm wide, 1.8 mm long. First femur, 2.5 mm; patella and tibia, 3.3 mm; metatarsus, 2.0 mm; tarsus, 1.2 mm. Second patella and tibia, 3.1 mm; third, 1.9 mm; fourth, 2.6 mm.

Variation. One male from the north slope of Alaska had a relatively smaller tegulum and a longer conductor and embolus in the palpus. As a result of the smaller tegulum, the loops of the duct were shallower. The specimen belongs to the Florida State Collection of Arthropods.

Diagnosis. The female can be separated from most larger North American *Pachygnatha* by the presence of a trichobothrium on the fourth metatarsus (Fig. 234); from *P. tristriata* by lack of a sclerite on the genital area (Fig. 229) and by the posteriorly broken dorsal abdominal markings (Fig. 232). The male is the only large North American species with a spur above the fang attachment on the chelicerae (Fig. 227), with a coiled duct in the tegulum (Fig. 235), and with the shape illustrated in Figs. 235, 237 of the palpal conductor. Half grown specimens have the trichobothrium on metatarsus 4.

Natural History. This species is found in wet areas (Wiehle, 1963). The egg-sac has been described by Wiehle (1963) and pictured by Nielsen (1932, fig. 358); it is attached to both bark and moss and is guarded. The young leave after only 2 weeks.

Distribution. Eurasia, Alaska to Manitoba (Map 7). One male from Washington, D.C. in the N. Banks collection may have been introduced.

Pachygnatha tristriata C. L. Koch
Plate 7; Figures 238–250; Map 7

Pachygnatha tristriata C. L. Koch, 1845, Arachniden, 12: 145, fig. 1066, ♀. Female from Pennsylvania in the Museum of the Humboldt University, Berlin, lost. Keyserling, 1884, Verhandl. Zool. Bot. Ges. Wien, 33: 656, pl. 21, fig. 8, ♀, ♂. McCook, 1893, American Spiders, 3: 270, pl. 26, fig. 6, pl. 28, fig. 1, ♀, ♂. Emerton, 1909, Trans. Connecticut Acad. Sci., 14: 202, pl. 5, fig. 6, ♀, ♂. Roewer, 1942, Katalog der Araneae, 1: 998. Kaston, 1948, Bull. Connecticut Geol. Natur. Hist. Surv., 70: 266, figs. 838, 839, 847, 848, ♀, ♂.

Description. Female. Carapace orange with longitudinal dark stripes and a dark band from thoracic depression anterio-laterally (Fig. 244). Chelicerae, sternum brown. Dorsum of abdomen with a gently curved black line on each side, farthest apart in middle (Fig. 244). Venter of abdomen above the genital area has a weakly sclerotized triangular patch, pointing anteriorly (Figs. 241, 245). The muscle impressions between the book-lung slits are barely visible and may be

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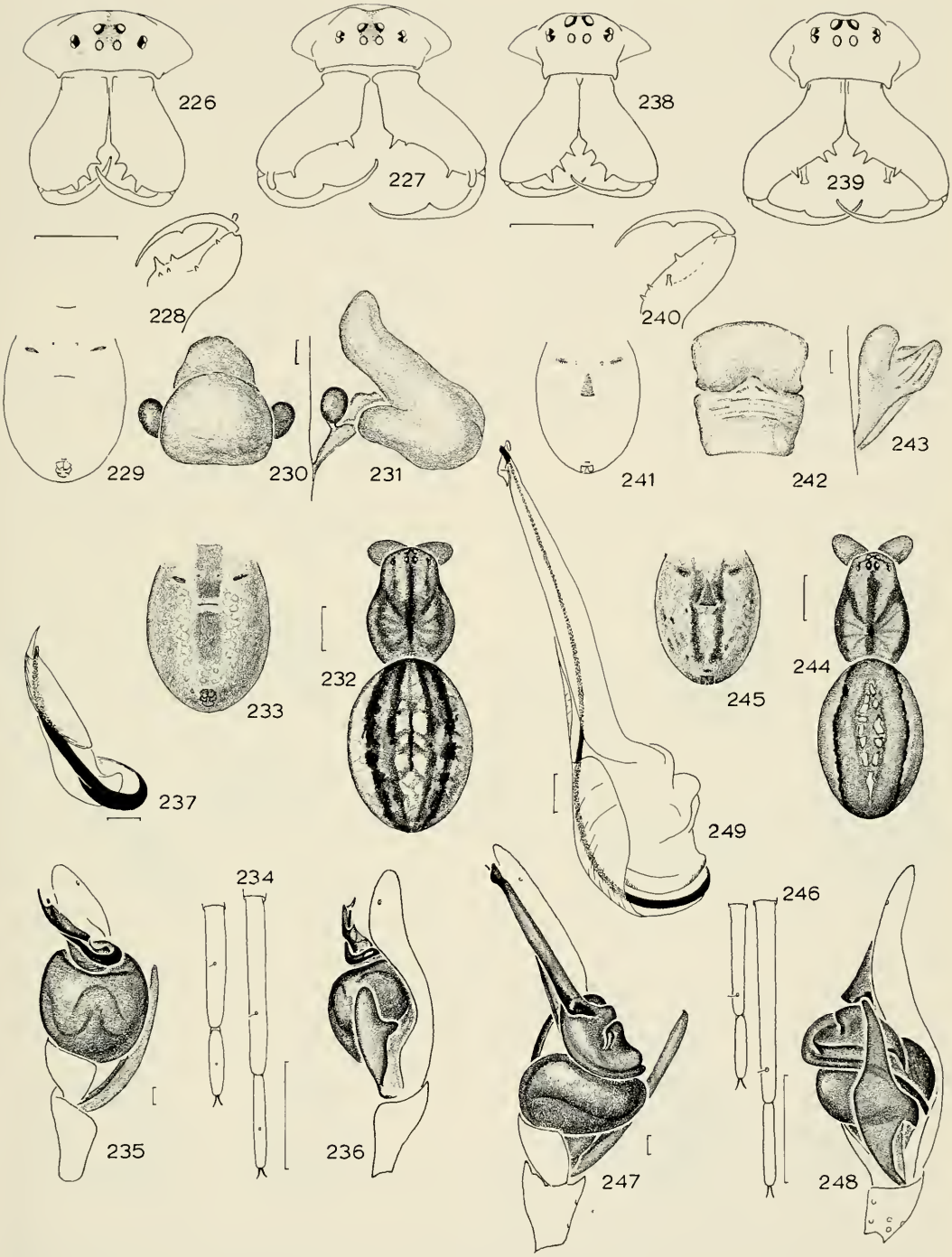
Figures 226–237. *Pachygnatha clercki* Sundevall. 226–228. Eye region and chelicerae. 226. Female. 227, 228. Male. 228. Left male chelicera, posterior. 229–234. Female. 229. Position of genital opening. 230, 231. Female genitalia. 230. Dorsal. 231. Lateral. 232. Dorsal. 233. Abdomen, ventral. 234. Left third and fourth metatarsi and tarsi, dorsal. 235–237. Left male palpus. 235. Ventral. 236. Lateral. 237. Embolus and conductor, ventral.

Figures 238–249. *P. tristriata* C. L. Koch. 238–240. Eye region and chelicerae. 238. Female. 239, 240. Male. 240. Left male chelicera, posterior. 241–246. Female. 241. Position of genital opening. 242, 243. Female genitalia. 242. Dorsal. 243. Lateral. 244. Dorsal. 245. Abdomen, ventral. 246. Third and fourth metatarsi and tarsi, dorsal. 247–249. Male palpus. 247. Ventral. 248. Lateral. 249. Embolus and conductor, ventral.

Scale lines. 0.1 mm; except Figures 226–229, 232–234, 238–241, 244–246, 1.0 mm.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split into three little platelets. One trichobothrium on distal end of both metatarsus 3 and 4 (Fig. 246). Total length, 6.0 mm. Carapace, 2.4 mm long, 1.7 mm wide. First femur, 2.3 mm; patella and tibia, 3.0 mm; metatarsus, 1.9 mm; tarsus, 0.9 mm. Second patella and tibia, 2.7 mm; third, 1.8 mm; fourth, 2.7 mm.

Male (from Massachusetts). There are three teeth on the anterior margin of the chelicerae (Fig. 239) and one blunt tooth on the posterior margin (Figs. 239, 240). Total length, 6.0 mm. Carapace, 2.7 mm long, 1.9 mm wide. First femur, 3.3 mm; patella and tibia, 4.1 mm; metatarsus, 2.7 mm; tarsus, 1.2 mm. Second patella and tibia, 3.6 mm; third, 2.2 mm; fourth, 3.4 mm.

Variation. Specimens from the southern part of the range are noticeably smaller than northern ones. Female total length, 4.9 to 6.5 mm; carapace, 2.3 to 2.9 mm long. Male total length, 4.5 to 6.2 mm; carapace, 1.9 to 2.9 mm long.

Diagnosis. The females can be separated from those of other species by the weakly sclerotized triangle on the genital area (Figs. 241, 245) and by the straight lines on the dorsum of the abdomen (Fig. 244). This species seems to lack seminal receptacles (Figs. 242, 243). The palpal conductor and embolus are much longer than those of other species (Figs. 247–249). The embolus is coiled (Fig. 247), and there is a unique blunt tooth on the posterior margin of the chelicerae (Figs. 239, 240).

Natural History. This species has been collected under a board in New Hampshire, while sweeping through vegetation, under stones, in an asparagus bed in Massachusetts, in a marshy meadow in New York, Bermuda grass pasture (*Cynodon dactylon*) in Louisiana, and in pitfall traps in Ohio and in a soybean field in Florida.

Distribution. Nova Scotia, Ontario, New England south to northern Florida, west to Wisconsin, Kansas and eastern Texas (Map 7).

Pachygnatha calusa new species
Figures 251–254; Map 7

Holotype. Male from Everglades, Florida, 27 December 1950 (A. M. Nadler) in the American Museum of Natural History. The name is a noun after the Indians of the Everglades.

Note. The small size of the unique specimen prevented studies of tracheae and trichobothria. It is uncertain whether the specimen belongs to *Pachygnatha* or *Glenognatha*. However, the description permits recognition.

Description. Carapace, legs yellow. Abdomen without markings. Posterior median eyes 0.8 diameters of anterior medians, laterals 0.6 diameters. Anterior median eyes slightly more than their diameter apart, slightly more than one diameter from laterals. Posterior median eyes slightly less than two diameters apart, 1.5 from laterals. The laterals are almost their diameter apart. The height of the clypeus equals two diameters of the anterior median eyes. The chelicerae have 3 small teeth on the anterior margin, 2 on the posterior (Fig. 251). The endites are widest distally. The third and fourth metatarsi have (probably) one trichobothrium, one-third the article's length from proximal end. The sternum connects to

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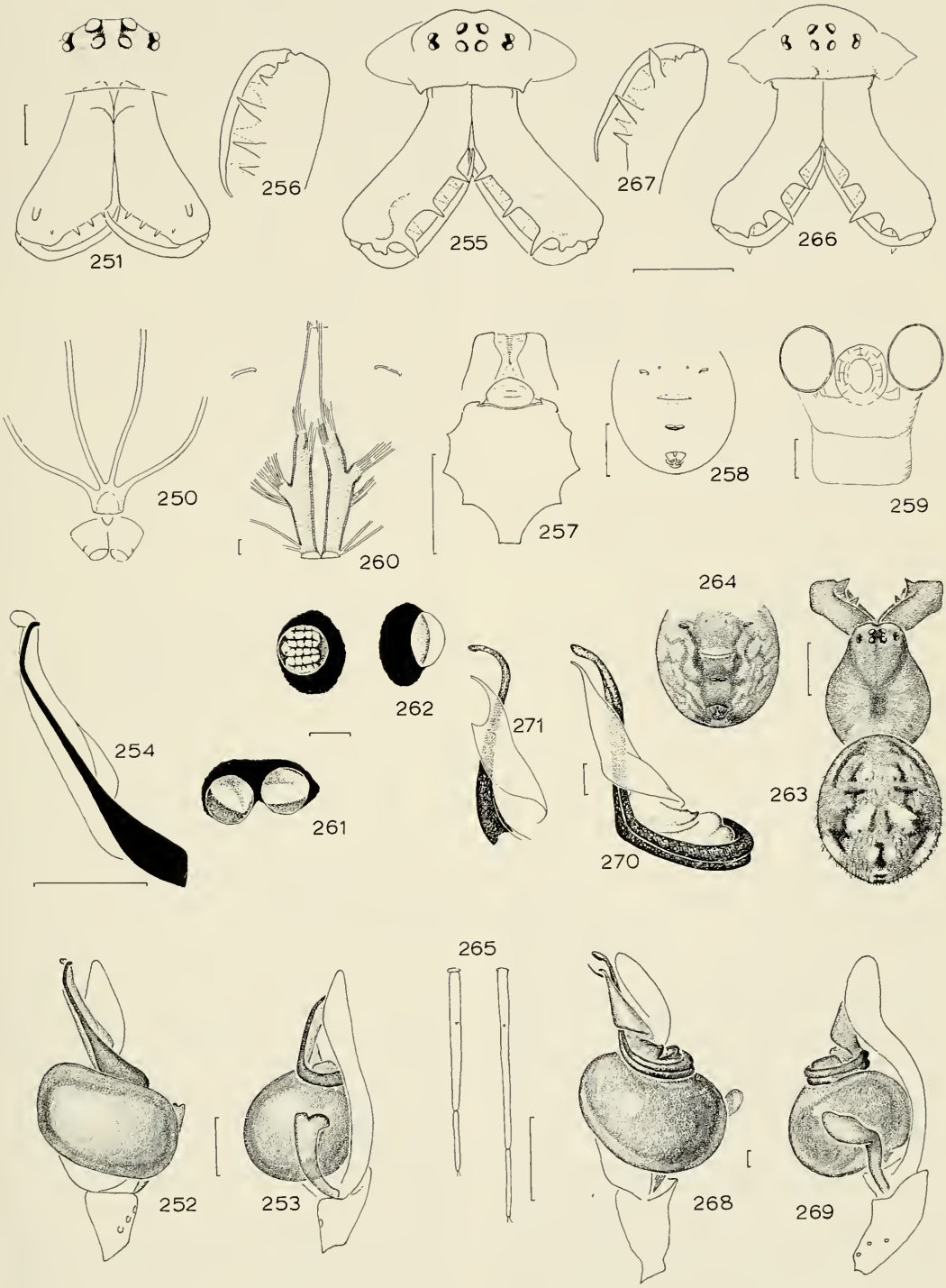
Figure 250. *Pachygnatha tristriata* C. L. Koch, tracheae.

Figures 251–254. *P. calusa* new species, male. 251. Eye region and chelicerae. 252–254. Left palpus. 252. Ventral. 253. Lateral. 254. Embolus and conductor, ventral.

Figures 255–271. *Glenognatha emertoni* Simon. 255–265. Female. 255. Eye region and chelicerae. 256. Left chelicerae, posterior. 257. Sternum, labium and endites. 258. Venter of abdomen. 259. Female genitalia, dorsal view. 260. Tracheae. 261. Left lateral eyes. 262. Posterior median eyes. 263. Dorsal. 264. Abdomen, ventral. 265. Left third and fourth metatarsus and tarsus. 266–271. Male. 266. Eye region and chelicerae. 267. Left chelicera, posterior. 268–271. Palpus. 268. Ventral. 269. Lateral. 270. Embolus and conductor, ventral. 271. Embolus and conductor tip, mesal.

Scale lines. 0.1 mm; Figures 255, 256–258, 263–267, 1.0 mm.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the narrow sclerite above the coxae between coxae 1 and 2, 2 and 3, 3 and 4. The abdomen is quite narrow; the spiracle is in advance of spinnerets, about the length of one spinneret. Total length, 1.9 mm. Carapace, 0.82 mm long, 0.62 mm wide. First femur, 1.19 mm; patella and tibia, 1.57 mm; metatarsus, 1.19 mm; tarsus, 0.52 mm. Second patella and tibia, 1.17 mm; third, 0.61 mm; fourth, 0.94 mm.

Diagnosis. The small size and distal notch on the paracymbium (Fig. 253) separate the species from *Pachygnatha brevis*.

Glenognatha Simon

Glenognatha Simon, 1887, Ann. Soc. Entomol. France, ser. 6, 7: 194. Type species by monotypy *G. emertoni* Simon. The name is feminine.

Mimognatha Banks, 1929, Bull. Mus. Comp. Zool., 69: 90. Type species by monotypy *Mimognatha foxi* (McCook). NEW SYNONYMY.

?*Hivaoa* Berland, 1935, Bull. B. P. Bishop Mus., 142: 50. Type species by original designation *H. argenteoguttata* Berland from Marquesas Islands. DOUBTFUL NEW SYNONYMY.

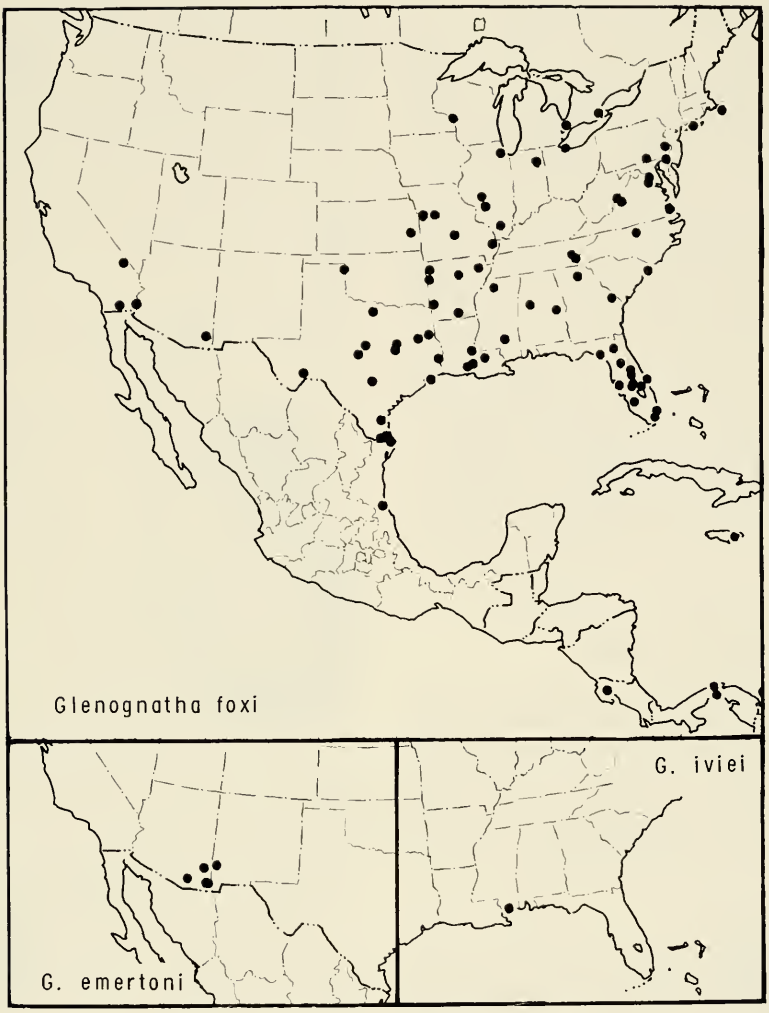
Diagnosis. Glenognatha differs from *Pachygnatha* by having the posterior ventral spiracle moved anterior (Figs. 258, 274), and by having an elaborate tracheal system: two large trunk tracheae that split into numerous fine tracheae (Figs. 260, 275). *Pachygnatha*, like most Araneidae, has the spiracle close to the spinnerets, and only four tracheae (Fig. 250). The abdomen of *Glenognatha* is softer and more spherical (Figs. 263, 264, 273, 274) than that of *Pachygnatha* and with paired light dorsal patches (Figs. 263, 273). *Glenognatha* differs from *Tetragnatha* by having a spherical abdomen and a canoe tapetum in the lateral eyes (Fig. 261).

Description. Carapace plain, usually darker than legs. Legs not banded. Dorsum of abdomen with paired light and dark marks, but no folium (Figs. 263, 273). Venter without distinct marks, darker gray in a longitudinal band in center (Fig. 264). Carapace smooth without setae, no distinct thoracic depression. Eyes closely grouped, median eyes their diameter apart, 1.5 diameters from laterals. Posterior median eyes may be slightly larger than others. *Glenognatha emertoni* has tapetum in the cells of the rhabdoms of the posterior median eyes (Fig. 262). Height of clypeus 2 to 3 diameters of anterior median eyes, more or less swollen on each side above chelicerae (Figs. 255, 266). Chelicerae large to very large, always with 3 teeth on the anterior margin, four on posterior (Figs. 255, 256, 266, 267). Those of male sometimes larger than female, at times with spur above base of fang (Figs. 276, 285). Labium large, endites short to long (Figs. 257, 274). Sternum does not usually surround coxae as in *Pachygnatha* (Fig. 257). All legs are thin and lack macrosetae (Fig. 273). The claws have long narrow teeth; accessory setae are present. Dorsally the base of the first and second femur has one (*G. foxi*) to 3 (*G. emertoni*) trichobothria, that of the third and fourth (*G. foxi*) femur has no trichobothria or has 4 and 5 (*G. emertoni*). Besides the several trichobothria on the tibiae, the metatarsi have one trichobothrium longer than the diameter of the article. The fourth metatarsus lacks a trichobothrium in *G. foxi*.

Males are the same size as females, as in *Pachygnatha*. The chelicerae are enlarged. The palpus is similar to that of *Pachygnatha*, with a spherical tegulum and a long, coiled embolus supported by a complex conductor (Figs. 270, 280, 289). The cymbium is narrow and the paracymbium a free sclerite, quite similar in shape in all species (Figs. 269, 279, 288).

The female genitalia are similar to *Pachygnatha* except that the median anterior chamber is spherical in *G. emertoni*.

Note. Banks (1929) placed *G. foxi* into its own genus because it has shorter chelicerae with only a few small teeth, and because of the very large spherical



Map 8. Distribution of *Glenognatha* species.

palpal tegulum and smaller embolus and conductor. I consider these specific differences. *Glenognatha foxi* males have enlarged chelicerae, and those of the female are not small. Many characters of *G. foxi* are associated with its small size: the relatively large eyes (Fig. 272), the convex sternum, and the great distance between the posterior coxae (Fig. 274). There are additional species in tropical America, some as small in size as *G. foxi*.

Natural History. The species live in more arid habitats than *Pachygnatha* species. The habits of *G. emertoni* are not known; *G. foxi* has been found in meadows and on hot, dry wastelands in Ohio. The unusual development of the tracheae and the forward movement of the spiracle is probably an adaptation against water loss. *Glenognatha foxi* is found on webs.

Distribution. The few *Glenognatha* species named are American, but there are specimens from the Pacific Islands in American collections.

KEY TO *GLENOGNATHA* SPECIES NORTH OF MEXICO

1. Less than 3.0 mm total length; female with chelicerae not enlarged (Fig. 272); male with spur on chelicerae (Figs. 276, 285); embolus and conductor minute on huge spherical tegulum (Figs. 278, 287); southern Canada to Central America and West Indies (Map 8) 2
– Total length more than 3.5 mm; female with chelicerae enlarged (Fig. 255); male without spur on chelicerae (Fig. 266); embolus and conductor length greater than height of spherical tegulum (Figs. 268); New Mexico, Arizona (Map 8) ..... *emertoni*
2(1). Female unknown; male with hooked tooth on anterior margin of chelicerae (Fig. 285); tip of embolus coiled (Fig. 289); Mississippi (Map 8) ..... *iviei*
– Male without hooked tooth on anterior margin (Fig. 276); tip of embolus not coiled (Fig. 280); southern Canada to Central America, West Indies (Map 8) ..... *foxi*

Glenognatha emertoni Simon
Figures 255–271; Map 8

Glenognatha emertoni Simon, 1887, Ann. Soc. Ent. France, ser. 6, 7: 194. Male holotype from Arizona in the Muséum National d'Histoire Naturelle, Paris, examined. 1894, Histoire Naturelle des Araignées, 1: 717, figs. 790, 791, ♂. Banks, 1913, Proc. Acad. Natur. Sci. Philadelphia, 65: 180, pl. 2, fig. 22, ♂. Roewer, 1942, Katalog der Araneae, 2: 995. Bonnet, 1957, Bibliographia Araneorum, 2: 1994.

Description. Female. Carapace, chelicerae, legs orange-brown; sternum brown. Dorsum of abdomen has paired gray spots alternating with paired light areas consisting of tiny white spots (Fig. 263). Clypeus swollen with two bulges (Fig. 255). Eyes subequal in size. Anterior median eyes slightly more than their diameter apart, two diameters from laterals. Posterior median eyes slightly more than their diameter apart, two from laterals. Posterior median eyes have tapetum inside rhabdoms which are in looped rows (Fig. 262). Endites are long but not wider distally. Chelicerae very large (Fig. 255). Abdomen spherical and hairy. Metatarsus 3 has trichobothrium one-third length of article from proximal end. Metatarsus 4 with trichobothrium one-third from proximal end. Total length, 4.7 mm. Carapace, 2.6 mm long, 2.0 mm wide. First femur, 3.3 mm; patella and tibia, 4.3 mm; metatarsus, 2.9 mm; tarsus, 1.4 mm. Second patella and tibia, 4.2 mm; third, 2.3 mm; fourth, 3.2 mm.

Male. Much like female. Chelicerae smaller and less modified (Fig. 266). Eyes slightly further apart. Total length, 4.0 mm. Carapace, 2.4 mm long, 1.9 mm wide. First femur, 3.2 mm; patella and tibia, 4.3 mm; metatarsus, 2.7 mm; tarsus, 1.5 mm. Second patella and tibia, 4.1 mm; third, 2.4 mm; fourth, 2.8 mm.

Variation. Female total length, 4.6 to 5.4 mm; carapace, 1.9 to 2.6 mm long. Male total length, 4.0 to 5.0 mm; carapace, 2.1 to 2.5 mm long.

Diagnosis. Glenognatha emertoni has a palpus (Figs. 268, 269) similar to that of *G. minuta* Banks found in Baja California; *G. minuta* is smaller in size, and the cheliceral shape and teeth differ. The larger size, large chelicerae readily separate *G. emertoni* from *G. foxi*. The seminal receptacles are unusually thin-walled and difficult to see (Fig. 259).

Natural History. Specimens have been found under rocks near streams and under rocks in nearly dry stream bed.

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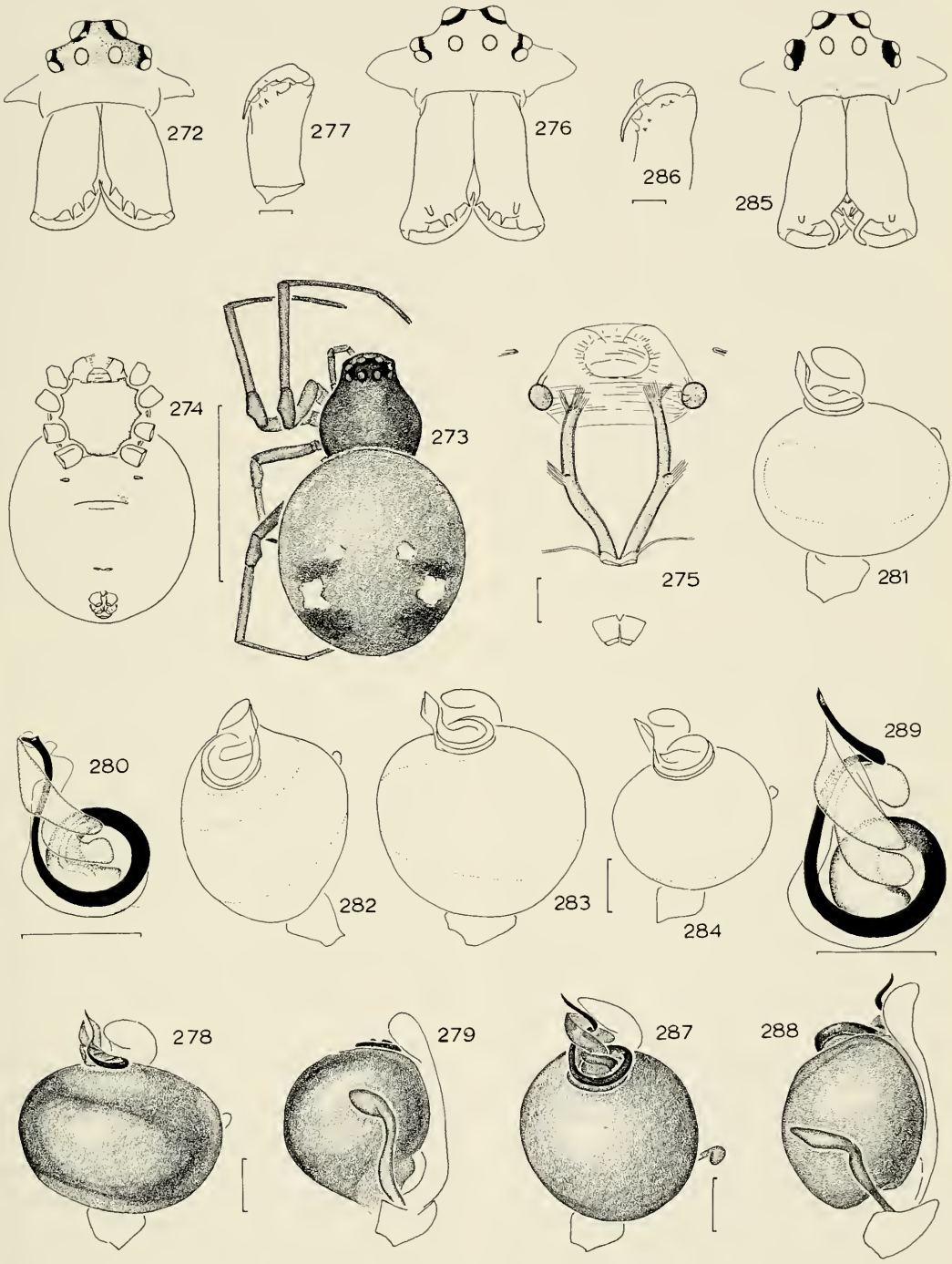
Figures 272–284. *Glenognatha foxi* (McCook). 272–275. Female. 272. Eye region and chelicerae. 273. Female. 274. Sternum, coxae and venter of abdomen. 275. Female genitalia and tracheae, dorsal view. 276–284. Male. 276. Eye region and chelicerae. 277. Left chelicera, posterior. 278–281, 283, 284. Left palpus. 278, 281–284. Ventral. 279. Lateral. 280. Embolus and conductor, ventral. 278–280. (Pennsylvania). 281. (Jamaica). 282, 283. (Arkansas). 284. (Panama Canal Zone). 282, 283. Right and left palpus from same individual.

Figures 285–289. *G. iviei* new species. 285. Eye region and chelicerae. 286. Left chelicera, posterior. 287–289. Palpus. 287. Ventral. 288. Lateral. 289. Embolus and conductor, ventral.

Scale lines. 0.1 mm; Figures 273, 274, 1.0 mm.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Distribution. New Mexico and Arizona (Map 8).

Glenognatha foxi (McCook)
Figures 272–284; Map 8

Theridium foxi McCook, 1893, American Spiders, 3, pl. 29, fig. 1.? *Nomen nudum.* Plate legend with comment: "No verbal description is made."

Mysmena bulbifera Banks, 1896, Trans. Amer. Entom. Soc., 23: 66. Three male, three female syntypes from Washington, D.C. in the Museum of Comparative Zoology, examined. 1904, Proc. Acad. Natur. Sci. Philadelphia, 56: 127, pl. 7, figs. 12, 13, ♂.

Glenognatha bulbifera:—Barrows, 1919, Ohio J. Science, 19: 210, figs. 1, 2, ♂ (mating, web).

Diplocephalus crumbi Petrunkevitch, 1925, J. New York Entomol. Soc. 33: 171, pl. 8, fig. 1, 2, ♂. Three male syntypes from Tennessee.

Glenognatha foxi:—Crosby and Bishop, 1928, Mem. Cornell Univ. Agric. Exp. Sta., 101: 1055.

Mimognatha foxi:—Banks, 1929, Bull. Mus. Comp. Zool., 69: 90. Crosby and Bishop, 1936, J. New York Ent. Soc., 44: 47. Kaston, 1948, Bull. Connecticut Geol. Natur. Hist. Surv., 70: 264, figs. 834, 835, ♀, ♂. Bonnet, 1957, Bibliographia Araneorum, 3: 2922.

Note. The name *foxi* has been used for this species for fifty years, although the McCook name lacked a description. His figure is adequate as an indication for a new species (Int. Code Zool. Nomenclature, Art. 16, vii).

Description. Carapace orange, sternum dark orange. Coxae, legs yellow. Dorsum of abdomen orange-white, sometimes with paired silver spots posteriorly and darker patches (Fig. 273); also some silver spots around anterior margin; venter without distinct markings. Eyes subequal in size; anterior medians 1.3 diameters apart, 1.5 diameters from laterals; posterior medians 1.1 diameters apart, 1.2 from laterals. Chelicerae have three teeth on the anterior margin, four on the posterior (Fig. 272). A tooth on posterior side of fang. Endites are not wider distally than at base. One trichobothrium on the metatarsi 1, 2 and 3, about one-quarter the article's length from proximal end. Total length, 1.6 mm. Carapace, 0.61 mm long, 0.56 mm wide. First femur, 0.67 mm; patella and tibia, 0.75 mm; metatarsus, 0.57 mm; tarsus, 0.36 mm. Second patella and tibia, 0.66 mm; third, 0.45 mm; fourth, 0.65 mm.

Male. Much like female. Chelicerae enlarged (Figs. 276, 277) and with spur above base of fang (Fig. 276). Total length, 1.8 mm. Carapace, 0.70 mm long, 0.63 mm wide. First femur, 0.81 mm; patella and tibia, 1.01 mm; metatarsus, 0.65 mm; tarsus, 0.36 mm. Second patella and tibia, 0.91 mm; third, 0.54 mm; fourth, 0.75 mm.

Variation. Some specimens have hardly any abdominal markings, some have scattered tiny white silver spots, and some have a pair of ventral silver patches between genital opening and spiracle. The size of the male spherical tegulum varies in size (Figs. 281–284) and left and right of the same individual may even differ slightly (Figs. 282, 283). Total length of females, 1.6 to 2.6 mm; carapace, 0.6 to 1.0 mm long. Total length of males, 1.4 to 2.2 mm; carapace, 0.6 to 1.0 mm long. The largest specimens came from Arizona and California.

Diagnosis. The small size, relatively small chelicerae (Figs. 272, 276) and the very large spherical tegulum of the male palpus separate this species from *G. emertoni* and other species. Unlike some similar tropical American species, the male has a spur above the fang on the chelicerae (Fig. 276). The tip of the embolus is not twisted (Fig. 280) as is that of *G. iviei.*

Natural History. Barrows (1919) found the spider in meadows and wastelands, in hot, dry situations. The spider makes a horizontal web 11 cm in diameter, 5 cm above the ground. Grass may grow through the web. The spiral strands are close together, and viscid silk is present. Spiders rest in the center of the web, and when disturbed drop to the ground and run away. Barrows observed mating in June in the center of the web, both individuals hanging down, the chelicerae locked and legs clasped. The palpal organs are inserted alternately every 5 minutes, copulation lasting 15 minutes.

Crosby and Bishop (1936) reported males collected in March and April by airplanes above Tallulah, Louisiana at 900 m and 60 m.

Other collections come from the edge of pond and saltmarsh in Massachusetts, from sweeping short grass in Virginia, from pitfall traps in a cornfield, sweet potato field, and a one-year-old abandoned field in North Carolina; from a web over a crawfish hole in Arkansas, a ground crevice in a dry lake in Missouri, and between stones on the bank of a stream "but did not notice an orb-web."

Distribution. The northernmost records are from Nantucket Island, Massachusetts, Wisconsin, Kansas, southern Arizona, southern California, south to Jamaica and Panama (Map 8).

Glenognatha iviei new species
Figures 285–289; Map 8

Holotype. Male from Gulfport, Mississippi, 28 August 1933 (W. Ivie, coll.) in the American Museum of Natural History. The species is named after Wilton Ivie, who collected the specimen and recognized that it was new.

Description. Carapace, sternum brown, legs light brown. Dorsum of abdomen mostly gray to black, with paired lighter patches lacking white or silver pigment. Venter gray, darkest in the center. Eyes subequal in size. Anterior median eyes slightly more than their diameter from each other and from laterals. Lateral eyes are on tubercles. One trichobothrium on third metatarsus only, one-third distance from proximal end. The fourth metatarsus appears to lack a trichobothrium. Total length, 1.4 mm. Carapace, 0.74 mm long, 0.65 mm wide. First femur, 0.78 mm; patella and tibia, 1.00 mm; metatarsus, 0.65 mm; tarsus, 0.41 mm. Second patella and tibia, 0.88 mm; third, 0.47 mm; fourth, 0.67 mm.

Diagnosis. Glenognatha iviei differs from *G. foxi* by the presence of an anterior hooked tooth on each chelicera (Fig. 285) and by the twisted tip of the embolus (Figs. 287, 289).

Azilia Keyserling

Azilia Keyserling, 1882, Verhandl. Zool. Bot. Ges. Wien, 31: 270. Type species by monotypy *A. formosa* from Peru. The name is feminine.

Note. According to Keyserling, the type specimens of *A. formosa* are in Warsaw, Poland. The staff of the Polish Academy of Sciences has not answered requests, thus the type may be lost. A neotype will have to be designated for *A. formosa* when the South American members of the genus are revised, since there is doubt on the identity of the species.

Diagnosis. Unlike all other Araneidae, except *Tetragnatha*, *Azilia* have the lateral eyes farther apart than the medians (Figs. 295, 300). The eyes are closely grouped and subequal in size. Unlike most Araneidae but like *Tetragnatha*, all eyes lack a tapetum (Figs. 299, 300). The oval abdomen (Figs. 295–297) separates *Azilia* from those *Tetragnatha* species which have separated lateral eyes. Unlike some other tetragnathids, there are no trichobothria on the base of the femora.

Description. Carapace streaked, darker on sides and head region; narrow in front. Eyes surrounded by black. Sternum dark, coxae light and legs banded. Abdomen streaked, often with white patch above spinnerets (Fig. 297). Eyes closely grouped, subequal in size, or posteriors slightly larger. Median eyes almost their diameter apart; anteriors almost touching laterals; posteriors about 1.5 from laterals; laterals about 2 diameters from each other. Eyes without tapetum, rhabdoms are in rows which loop (Figs. 299, 300). Clypeus height equal to or slightly less than diameter of anterior median eyes (Fig. 294). Chelicerae strong but not enlarged as in *Pachygnatha* or *Glenognatha*. Endites long, widest distally (Fig. 298); legs fairly long with macrosetae (Fig. 295). No trichobothria on base of femur. Abdomen ovoid, widest anteriorly (Fig. 295), often with a hump above spinnerets (Fig. 297).

Males slightly smaller than females with stronger macrosetae on legs.

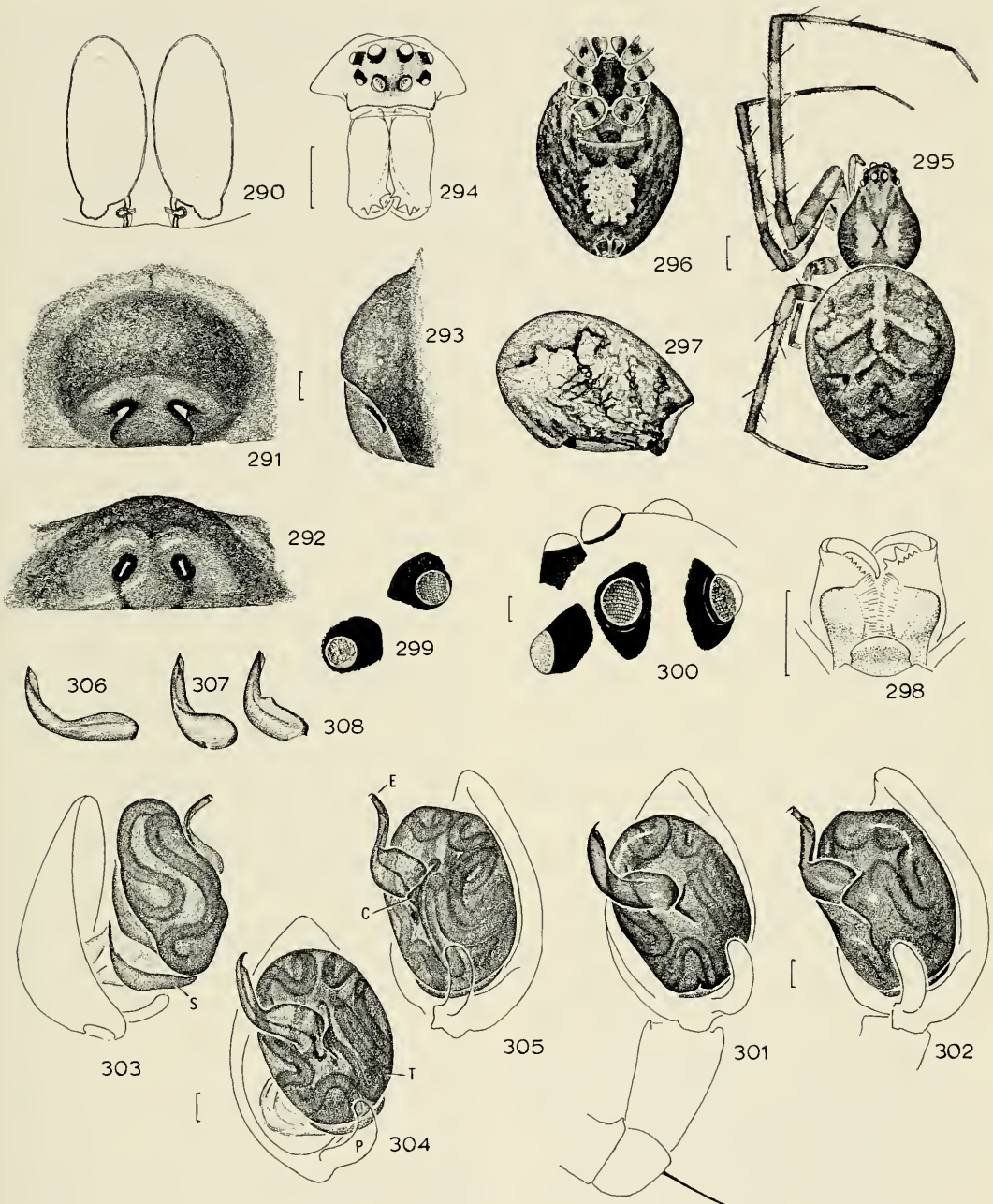
Genitalia. There is an epigynum

Plate 8. *Azilia affinis* O. P.-Cambridge. Web, diameter about 12 cm; note the closed hub (photo M. Stowe).

present (Figs. 291–293), but the openings face posterior as in *Meta*. The seminal receptacles (Fig. 290) are very thin-walled like those of *Leucauge*. The palpus is very simple (Figs. 301–305) with tegulum (T) and embolus (E), but it lacks a distinct conductor. The paracymbium (P in Fig. 304) is only little modified.

Natural History. All species are found in dark places and caves, like many *Meta*. It is interesting that, despite the crepuscular habits, the eye of the spider lacks a tapetum. The web is vertical to horizontal and loose. The hub, unlike that of *Meta*, *Leucauge* and *Tetragnatha* webs, is closed (Plate 8). The spider hangs on the underside of the web and bounces when disturbed (S. Peck, personal communication).

Relationship. Like other genera in



Figures 290–308. *Azilia affinis* O. P.-Cambridge. 290–300. Female. 290. Female genitalia, dorsal view. 291–293. Epigynum. 291. Ventral. 292. Posterior. 293. Lateral. 294. Eye region and chelicerae. 295. Female. 296. Abdomen, ventral. 297. Abdomen, lateral. 298. Labium and endites. 299. Left lateral eyes. 300. Posterior median eyes and left laterals. 301–308. Left male palpus. 301. Ventral. 302. Lateral. 303–305. Expanded and cleared. 303. Mesal. 304. Ventral. 305. Lateral. 306–308. Embolus. 306. (Florida). 307. (Georgia). 308. (Southern Texas).

Scale lines. 0.1 mm; Figures 294–298, 1.0 mm.

Abbreviations. C, conductor; E, embolus; P, paracymbium; S, subtegulum; T, tegulum.

Map 9. Distribution of *Azilia affinis* O. P.-Cambridge.

this paper, the placement of *Azilia* is difficult. The palpus and the non-sclerotized seminal receptacles resemble *Leucauge* superficially. The shape of the abdomen and coloration resemble *Meta*. Only *Tetragnatha* also lacks a tapetum in all eyes. The long endites are tetragnathid-like, but in other genera long endites are usually accompanied by enlarged chelicerae. The solid hub of the web is unlike any other web of *Meta*, *Leucauge* or *Tetragnatha* relatives.

Species Differences. The species differ in the ventral marking of the abdomen, and the shape of the epigynum and palpus. Unlike those of *Leucauge* and *Pachygnatha*, the differences between species are considerable, although all can be recognized as *Azilia* by the unusual eye arrangement.

Distribution. There are only 4 or 5 species in tropical America, of which only one, *A. affinis*, extends its range into temperate North America (Map 9).

Azilia affinis O. P.-Cambridge
Plate 8; Figures 290–308; Map 9

Azilia affinis O. P.-Cambridge, 1893, Biologia Centrali-Americana, Araneidea, 1: 115, pl. 15, fig. 4, ♀. Female holotype from Teapa, Tabasco, Mexico in British Museum, Natural History, examined.

Azilia vagepicta Simon, 1895, Ann. Soc. Entomol. France, 64: 153. Female specimens from "Amer. sept, Georgia," in the Muséum National d'Histoire Naturelle, Paris, examined. Banks, 1913, Proc. Acad. Natur. Sci. Philadelphia, 65: 180, pl. 11, fig. 14, ♀. Roewer, 1942, Katalog der Araneae, 1: 923. Bryant, 1945, Trans. Connecticut Acad. Arts Sci. 36: 208, fig. 10, ♂. Bonnet, 1955, Bibliographia Araneorum, 2: 840. NEW SYNONYMY.

Azilia mexicana Banks, 1898, Proc. California Acad. Sciences, ser. 3, 1: 258, pl. 15, fig. 19. Adult syntypes in California Academy of Sciences, destroyed, one subadult male and one juvenile syntype from Tepic, Mexico in the Museum of Comparative Zoology, examined. NEW SYNONYMY.

Description. Female from Alachua County, Florida. Dorsum of abdomen indistinctly patterned with dark chevrons posteriorly and light areas consisting of tiny white pigment spots. Sides with dark anastomosing streaks. Venter with a square central light patch consisting of scattered tiny white pigment. Thorax with an X-shaped depression (Fig. 295). The epigynum has two openings and very weakly sclerotized seminal receptacles (Figs. 290–293). Total length, 8.9 mm. Carapace, 3.5 mm long, 2.5 mm wide. First femur, 6.0 mm; patella and tibia, 7.3 mm; metatarsus, 6.4 mm; tarsus, 1.9 mm. Second patella and tibia, 5.3 mm; third, 3.2 mm; fourth, 4.7 mm.

Male from Alachua County, Florida. Color like female. Smaller than female but similar structure. Anterior part of X-shaped thoracic mark less distinct than posterior. Eye sizes and spacing as in female. Chelicerae like those of female. Tooth on the distal end of the palpal femur. No tooth on the endite and no proximal tooth on femur. None of the legs is modified, but the macrosetae are relatively longer than those of the female. Total length, 6.8 mm. Carapace, 3.2 mm long, 2.4 mm wide. First femur, 8.0 mm; patella and tibia, 10.0 mm; metatarsus, 9.7 mm; tarsus, 2.3 mm. Second patella and tibia, 6.7 mm; third, 3.0 mm; fourth, 4.9 mm.

Variation. The posterior hump is more distinct in some specimens (Fig. 297) than others, almost absent in specimens from Florida. No two populations have similar genitalia, but the differences

in the epigynum are minor. The differences of the palpi are in the shape of the embolus (Figs. 306–308) and the width of the bulb; also, no two males have a similar duct coil within the bulb (Figs. 303–305).

Females vary in total length from 6.9 to 9.9 mm; carapace, 2.9 to 3.8 mm long, 2.1 to 2.8 mm wide; first patella and tibia, 6.3 to 8.1 mm long. Males vary in total length from 5.2 to 6.9 mm; carapace, 2.6 to 3.9 mm long, 1.9 to 2.4 mm wide; first patella and tibia, 6.3 to 9.4 mm long.

Diagnosis. Azilia can be separated from other Central and South American species by its prominent square, light patch on the venter of the abdomen (Fig. 296), the openings of the epigynum (Figs. 291–293), and its large size. The males of related species are mostly unknown; one has a long filiform embolus.

Natural History. Azilia vagepicta has been collected in caves and wood rat nests (*Neotoma micropus*) and in other presumably dark situations, including mesic lush ravine; mesic woods, shady recesses on the sides of a building structure, mesic hammock, in bottom of wet ravine, and in dried-up cypress-hardwood swamp. Many were collected at night with flashlight. In Florida, the species occurs in twilight zones of caves, where the spiders feed on fungus gnats. Orb-webs are vertical to horizontal (Plate 8).

Distribution. Georgia, northern Florida, Gulf states, Mexico to Costa Rica (Map 9).

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ZOOGEOGRAPHY OF NORTH AMERICAN UNIONACEA (MOLLUSCA: BIVALVIA) NORTH OF THE MAXIMUM PLEISTOCENE GLACIATION

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ZOOGEOGRAPHY OF NORTH AMERICAN UNIONACEA (MOLLUSCA: BIVALVIA) NORTH OF THE MAXIMUM PLEISTOCENE GLACIATION

RICHARD I. JOHNSON[1]

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ABSTRACT. The Unionacea (Mollusca: Bivalvia) now found north of the maximum Pleistocene glaciation in North America (which extended roughly to the Missouri and Ohio rivers in the west and to the New York–Pennsylvania boundary in the east), excluding two species of western origin, migrated there from southern refugia and are not autochthonous. The probable origins and likely migration routes of the unionids found in that northern region are discussed with special emphasis on their movements within the American Interior Basin.

In addition to a ubiquitous fauna widely dispersed in both the Mississippi and Ohio rivers, and found on both the Ozark and Cumberland plateaus, each plateau has a unique assemblage of species. The post-glacial migration of some of these Ozarkian, Cumberlandian, and Ohioan species accounts for the differences in the faunas of the Mississippi River above the Missouri River (Mississippian Region) and the Ohio River drainage (Ohioan Region). Tables list the faunas of the several river systems and the species are listed to indicate their probable refugia. Fourteen species are monographed and in-

clude their known distributional records. Eight of these are found only in the Ozarkian Region. Among the additional six species, two other Ozarkian species are included which extended their ranges in post-glacial time, *Lampsilis higginsi* and *Proptera capax*. *Lampsilis higginsi* and *abrupta*, a closely related Cumberlandian species, are compared. They illustrate overlapping distribution in the Mississippian and Ohioan regions. *Cyprogenia stegaria*, a Cumberlandian species which extended its range into the Ohioan Region, is compared with *C. aberti*, an Ozarkian species. *Arcidens confragosus* and *Anodonta suborbiculata*, which extend south to the Gulf Coastal Region, are examples of species that entered the Ohioan Region from the West. The repopulation of the St. Lawrence River system by species from the Ozarkian, Mississippian, Cumberlandian, Ohioan, and Northern Atlantic Slope regions is discussed as is the repopulation of the Canadian Interior Basin.

INTRODUCTION

This paper brings together the available data on the distribution of the Unionacea found north of the maximum Pleistocene glaciation in North America (roughly to the Missouri and Ohio rivers in the west and to the New York–Pennsylvania boundary in the east). Much of this vast area was repopulated within approximately the past ten thousand years during the retreat of the Wisconsin ice sheet. Many of the dispersal routes have been documented, but no previous paper discusses the probable refugia of the species, or lists the known faunas of the relevant river systems.

It should be mentioned that the mobility, and thus the means of dispersal, of the Unionacea is passive. It is dependent on the temporary attachment of the larval forms (glochidia) onto passing fish.

ZOOGEOGRAPHY OF NORTH AMERICAN UNIONACEA NORTH OF THE MAXIMUM PLEISTOCENE GLACIATION

Introduction. Prior to the Cretaceous Period the then Cumberland Plateau extended continuously from the Appalachian Mountains southwest into western Texas. The Mississippi River did not exist. What is remarkable about the present unionid faunas on the Ozark Plateau, on both sides of the Ozark Crest, and on the Cumberland Plateau, is their similarity, even after the passage of some 200 million years. The maximum Pleistocene glaciation extended southward, west of the Appalachian Mountains, roughly to the present Missouri and Ohio rivers, and to the Pennsylvania–New York boundary in the east. During the Nebraskan glacial stage, which represents the earliest and most southerly extension of the ice sheet, the unionid fauna was eliminated north of this line. With the exception of two species from the Pacific Coastal Region, the Interior Basin (including the Canadian Interior Basin), the St. Lawrence River system, and the Northern Atlantic Slope, have since been repopulated with species from southern refugia.

Ozarkian Region. The upper portions of the Red River system, Oklahoma and Arkansas; Black River system, Arkansas; Arkansas River system, Kansas, Oklahoma, and Arkansas; White River system, Missouri and Arkansas; St. Francis River system, Missouri and Arkansas, all below the Ozark Crest; and the Osage, Gasconade, and Meramec river systems, all in Missouri, and all above the Ozark Crest; contain an assemblage of 8 species of Unionidae found nowhere else (Tables 1, 5 E). These river systems comprise the Ozarkian Region (H. and A. van der Schalie, 1950: 450, map 1 IV).

In addition to these 8 species (Table 5 E) there are two others, *Lampsilis higginsi* and *Proptera capax*, which have spread beyond into the Mississippian and Ohioan regions, the latter also into the Lake Erie drainage of the St. Lawrence River system. Four species (Table 5 D) occur in the Ozarkian and Cumberlandian regions which are not found in the Mississippian Region. Nine species (Table 5 C) found in the Ozarkian are not found in the Mississippian or in the Cumberlandian regions but are found in the Gulf Coastal Region. Nine species (Table 5 B) found in the Gulf Coastal and Ozark-

ian regions are also found in the Mississippian and Ohioan regions. With the exception of *Lampsilis radiata siliquoidea* in the Cumberlandian Region, 40 species (Table 5 A) occur in the Meramec River system, which are generally distributed in both the Mississippian and Ohioan regions.

Cumberlandian Region. Ortmann (1924a: 40) defined the Cumberlandian Region to include: the drainages of the Tennessee River system from the headwaters to the vicinity of Muscle Shoals, in Colbert and Lauderdale counties, Alabama; and the Cumberland River system from the headwaters to the vicinity of Clarksville, Montgomery County, Tennessee (Ortmann, 1925: 366). Ortmann (1924a: 40) discussed the unionid fauna of the Duck River drainage, which is at present, a tributary of the Tennessee River system. The upper portion of the Duck River has a fauna that is 38 percent Cumberlandian. Ortmann suggested that this was the original fauna and that there once had been stream confluence with it and both the Tennessee and Cumberland river systems.

Originally Ortmann (1924a: 40) regarded as Cumberlandian only those unionid species currently confined to the areas of the Tennessee and Cumberland river systems as defined above. This Cumberlandian fauna consists of 30 species (Table 1). All but one of these occur in the Tennessee River, and 21 are also found in the Cumberland River. Later Ortmann (1925: 370) suggested that there were Cumberlandian species that had descended the Tennessee and/or Cumberland rivers and invaded the Ohio drainage, though he never indicated which they were. Table 2, C indicates that the following are those additional Cumberlandian species:

52 *Lampsilis abrupta*
40 *Carunculina glans*
20 *Plethobasus cicatricosus*
46 *Plagiola personata*
47 *Plagiola flexuosa*
43 *Plagiola sampsoni*
44 *Plagiola propinqua*

See appropriate number under: Unionacea of the Mississippian and Ohioan Regions With Refugia in Tributaries of the Missouri and Ohio rivers on Their South Side [List 1].

Thirty-seven of the 90 species of unionids found in the Tennessee River are Cumberlandian, as are 27 of the 78 found in the Cumberland River. These two assemblages are the largest number of unionid species found in any of the world's rivers.

Mississippian Region. H. and A. van der Schalie (1950, map 1) regarded as the Interior Basin (or Mississippian Region), all of the river in the Gulf Coastal Region, from the Rio Grande to and including the Mobile-Alabama-Coosa River; the entire Mississippi River system, including the Ohio; the Canadian Interior Basin; and the St. Lawrence River system west of Lake Erie. Excepted were the Ozarkian and Cumberlandian regions as defined above.

The Mississippian Region is more narrowly defined here to include: the Missouri River and all those rivers draining into its south side, excluding the Osage, Gasconade, and Meramec river systems which are in the Ozarkian Region; the Blackwater River since it has no Ozarkian species in it; and all of the Mississippi River, above the Missouri, and the rivers flowing into it west and north of the Ohio River. In this area, as thus defined, occur 53 species of Unionacea; 40 are so uniformly distributed, in both the Mississippian and Ohioan regions, that little can be said of their general zoogeography. All of them occur in the Meramec River system, which may have been the major refugium for these species west of the Ohio River (Table 2 A). With the exception of *Margaritifera falcata*, from the Pacific coastal Region, 11 other species had refugia below the Ozark Crest, and five also had a refugium in the Meramec River.

These 11 western species penetrated the Ohioan Region to some extent, yet only one Ohioan and one Cumberlandian species occur in the Mississippian Region. During the Wisconsin glacial stage (Plate 1), the ice sheet in the Mississippian Region was much less extensive than in the Ohioan Region, and perhaps, the former fauna had achieved a stability that prevented the newly available Ohioan fauna from penetrating it.

Ohioan Region. This area consists of all the rivers that flow into the Ohio River, excluding the Tennessee and Cumberland rivers.

There are 72 species of Unionacea in this area, 40 of which are found in the Mississippian Region as well (Table 2, A). The Green, Salt, and Kentucky rivers, on the south side of the Ohio, are each fairly well represented by this group of species; but the Tradewater, Licking, and Big Sandy rivers are not, suggesting that these were repopulated in post-glacial time. In addition to the seven species found in the Ohio River drainage, regarded above as Cumberlandian, are 16 additional species that appear to be of Ohioan origin (Table 2, C). With the exception of *Lasmigona compressa*, missing in the Tennessee, Cumberland, and Green rivers, all the other species occur in the Tennessee River, and most are also found in the Cumberland and Green rivers.

Ortmann (1926: 186) concluded that "there is a sharp line between the Cumberland and Green rivers in southern Kentucky separating two apparently old faunas, the Cumberlandian and Ohioan." Ortmann (1913: 382) had previously indicated that the Kentucky, Licking and Big Sandy rivers contained Ohioan species (Table 2, C) and suggested that the uniformity of the fauna of the upper Ohio basin was a character acquired in post-glacial time. He further noted that remnants of the pre-glacial Ohioan fauna may have had refugia in the Kanawha, Monongahela, and [Allegheny] rivers.

Table 2, C indicates that the Tennessee and Cumberland rivers were major refugia of both Cumberlandian and Ohioan unionid species, and the Green River was a major refugium for the Ohioan species. These rivers appear to be the most important refugia for those species that repopulated the Wabash and Greater Maumee rivers (Plate 1, D).

Table 2, B shows the distribution of 11 Mississippian unionids that penetrated the Ohioan Region. Most of these species penetrated at least to the Wabash River drainage.

St. Lawrence River System. The St. Lawrence River system has no natural connections with the Mississippi or Ohio river systems, and flows for some 2,000 miles east to the Atlantic Ocean. Walker (1913: 18) studied the distribution of the unionids found in the Great Lakes.

Lake Superior. Walker found *Elliptio complanata*, an Atlantic Slope species, in Lake Superior, at the western extremity of the St. Lawrence River system. He suggested that this species arrived in this area by way of the Mohawk and Trent outlets into Georgian Bay of Lake Huron and from there into Lake Superior (Walker, 1913: 58). Ortmann (1924b) confirmed this, pointing out that toward the end of glacial time, Lakes Superior, Michigan, and Huron (then Lake Algonquin IV) flowed through the Trent Valley from Georgian Bay, Lake Huron, directly into Lake Ontario (then Lake Iroquois). Later the North Bay outlet opened, allowing the water to flow from the end of Georgian Bay through the Ottawa Valley to the Ottawa Sea. After the weight of glacial ice was removed by further melting, the Ottawa Valley was sufficiently elevated to eliminate it as an outlet.

Clarke (1973: 40) pointed out that *E. complanata* has a continuous distribution in the Hudson Bay drainage from the Moose River system in northwestern Quebec and northeastern Ontario to the headwaters of the Albany River system in northwestern Ontario. Since the head-

waters of the Albany River are *still* connected to Lake Superior through Long Lake and Lake Nipigon, there can be little doubt that this route also served in the post-glacial migration of *E. complanata* into Lake Superior.

Lake Michigan. Van der Schalie (1963) established that a number of unionid species found in the Millecoquin River, in the eastern part of the Upper Peninsula of Michigan, the Carp and Ocqueoc rivers, in the northern part of the Lower Peninsula, presently draining into Lakes Michigan and Huron; indicate that these rivers were once connected to the now submerged Mackinac River system. This system received its fauna from the Fox River which was then connected to the Wisconsin River in the vicinity of Portage, Columbia Co., Wisconsin (Plate 1, B). He further established that the present distribution of the unionids in the rivers of western Michigan indicate that before the formation of Lake Michigan, the rivers of western Michigan (e.g. the Muskegon, Grand, and St. Joseph) connected with the Des Plaines River through the Chicago Outlet and Illinois River to the Mississippi (Plate 1, C). He also deduced that the Muskegon River was at one time a tributary of the Grand River (of western Michigan) and also that the fauna of the Saginaw, now flowing into Lake Huron, was derived from the previously mentioned Grand River during the confluence of the former drainages (van der Schalie, 1961: 157).

Lake Erie. Ortmann (1924b) pointed out that during the Trent Stage of the Wisconsin, the Maumee River flowed through the partially dry bed of Lake Erie into the Wabash River. The Maumee and Wabash rivers were connected in the vicinity of Fort Wayne, Allen Co., Indiana (Plate 1, D). It was by this route that 43 species of unionids (Table 3, A), from the Mississippian, Cumberlandian, and Ohioan faunas, found their way into the Greater Maumee drainage. Many of these species are not found in Lake Erie proper. On the basis of the unionid faunas of rivers now flowing into Lake Erie, Ortmann concluded that the Huron and Raisin rivers in Eastern Michigan; the Sandusky, Vermilion, Lower Cuyahoga and Grand rivers in Ohio; as well as the Grand River in Ontario were once part of the Greater Maumee drainage. Van der Schalie (1938), also on the basis of unionid distribution, concluded that the Clinton River, which flows into Lake St. Clair, was also part of the Greater Maumee drainage; but he determined that the Rouge River, between the Clinton and Huron rivers, was of later origin (Figure 1).

Lake Ontario. This, the newest of the Great Lakes, has a unionid fauna of seven species. Two are Atlantic Slope species. Clarke and Berg (1959: 3) monographed the species found in this lake and those of the Genesee River and Finger Lakes Basin which flow into it on its south side, and suggested that the Atlantic Slope species found there were derived from the Susquehanna Basin by way of glacial Lake Newberry. When the Wisconsin ice sheet melted, the Finger Lakes Basin was inundated by Lake Newberry which, in its earlier stages, drained southward into the Susquehanna drainage basin (Plate 1, E). As the glacier continued to recede a lower channel was uncovered and the water drained westward into the Erie Basin. Later, when an even lower outlet was uncovered, the lake in the Erie Basin merged with the Finger Lakes Basin and flowed eastward into the Mohawk and Hudson river valleys (Plate 1, F).

Lake Champlain. Simpson (1896: 381) suggested that sometime since the end of the Wisconsin, there had been a connection between the Hudson River and Lake Champlain when the Erie Basin merged with the Finger Lakes Basin and flowed eastward into the Mohawk and Hudson river valleys. He further suggested that the Lake Champlain fauna may have been derived from the St. Lawrence Riv-

Figure 1. Trent outlet stage of the Great Lakes. (After Ortmann, 1924, fig. 2.)

The darkened area represents the melt water which flowed through the Trent Outlet into the Mohawk River (arrow). The Greater Maumee River system is postulated, and the rivers which formed part of it are numbered. 1. Clinton, 2. Huron, 3. Raisin, 4. Sandusky, 5. Vermilion, 6. lower Cuyahoga, 7. Grand River, Ohio, 8. Grand River, Ontario. The arrow between 3 and 4 represents the flow of the Maumee River system into the Wabash.

er by way of the Richelieu River. Since the present fauna, with the exception of *Elliptio complanata*, is from the west, this second explanation is more probable.

Ottawa River. It is assumed that the large number of Atlantic slope species in the Ottawa River are derived from the southern side of the lower St. Lawrence River, but this is not documented here.

Canadian Interior Basin. (Plate 1, Insert.) North of the Mississippian Region and the St. Lawrence River system, this vast region comprises more than one third of North America. It is divided into the Arctic and Hudson Bay drainages. The latter has a number of natural connections with the St. Lawrence River system. The Albany River system in Ontario is joined to Lake Superior by Lake Nipigon and Long Lake, both of which have north and south flowing outlets. The Rainy River–Winnipeg River system is similarly joined to Lake Superior at Saganaga [Seiganagah] Lake which drains both east and west (Clarke, 1973: 6). Most of the unionid fauna of the Canadian Interior Basin is of Mississippian origin (Table 4). Thirteen of the 16 species in the Hudson Bay drainage are derived from a former confluence of the Minnesota River, of the upper Mississippi, and the Red River of the North (Plate 1, A). Prior to the recent erection of dams, these rivers were periodically joined by floods (Dawley, 1947: 680). Three of these 13

species were also derived from the St. Lawrence River system, and an additional species was described exclusively from the latter system. One species is from the Pacific Coastal region and one appears to be speciating in the area. Only three of the 16 species occur in the Arctic Region.

Pacific Coastal Region. This consists of rivers that flow into the Pacific Ocean to, and including, Alaska which was unglaciated. The unionid fauna is comprised of eight species, two of which are found outside of the region.

Northern Atlantic Slope Region. The unionid fauna of the Northern Atlantic Slope consists of 15 species, all of which had refugia south of the Terminal Moraine. This also includes one subspecies, *Anodonta cataracta fragilis* found in Newfoundland, New Brunswick and Nova Scotia.

FAUNAL STUDIES

The tables in this paper are based mostly on reliable published records, and on specimens in the Museum of Comparative Zoology, or elsewhere, as noted.

Ozarkian Region. The unionid fauna of the Red River system was enumerated by Isely (1925), Strecker (1931), and by Valentine and Stansbery (1971). The unionids of the Ouachita River drainage of the Black River system were listed by Wheeler (1918). The unionids of the upper tributaries of the Arkansas River system in Kansas were studied by Scammon (1906), Clarke and Gillette (1911), and again by Murray and Leonard (1962). The unionids of the tributaries of the Neosho River drainage in Missouri were listed by Utterback (1917), and those of the Arkansas River system in Oklahoma by Isely (1925). The unionids of the White and Black river drainages of the White River system in Missouri were monographed by Utterback (1915–1916), and those of the White River in Arkansas were studied by Call (1885). Meek and Clark (1912) listed the unionids of the Big Buffalo Fork, and Wheeler (1914) those of the Cache River, both tributaries of the White River in Arkansas. Utterback (1917) listed the unionids of the St. Francis River system in Missouri, and Call (1885) studied those in Arkansas. The unionid faunas of the Osage, Gasconade, and Meramec rivers were summarized by Utterback (1917) in a table. A recent report by Buchanan (1977) based on extensive collections from the Meramec River was very useful in establishing its fauna. Buchanan (1980) later added *Anodontoides ferussacianus* and *Simpsoniconcha ambigua* to the Meramec River fauna. Gordon, *et al.* (1980), while primarily interested in the unionids of Arkansas as a political unit, added a number of records to several of the Ozarkian river systems. The faunas of the Osage and Gasconade rivers, as well as some of the drainages south of the Ozark Crest, were augmented by records made by the 1964 Harvard-Ohio State Museum expedition to this area.

Mississippian Region. The unionids of the upper Missouri River were studied by Coker and Southall (1915). West of the Osage River, and like it flowing into the Missouri River on its South side, is the Blackwater River. Since, according to Utterback's (1917) table its fauna includes no Ozarkian species, it properly belongs in the Mississippian Region. The distribution and number of unionid species in the Mississippi River, discussed by H. and A. van der Schalie (1915), was based on several mussel surveys made in the Mississippi River, including one by Grier and Mueller (1922–23), and on the extensive collection made by Max. Ellis during 1930–31.

Baker's (1928) monograph of the Wisconsin mollusks was useful in establishing the fauna of the Wisconsin and Fox rivers, as was Dawley's (1947) report which enumerated the fauna of the Minnesota River and mentioned its relation-

ship to the Red River of the North. The present (1973–77) distribution of the unionids of the upper Mississippi River in Wisconsin was made available by Mathiak (1979). The fauna of the Illinois River, past and present, was studied by Starrett (1971). The unionids of its tributaries in the Kanakee Basin had been enumerated by Wilson and Clark (1912). A popular work by Parmalee (1967) on the freshwater mussels of Illinois also contained useful records.

Cumberlandian Region. Ortmann (1918) reported on the unionid fauna of the upper Tennessee River. Subsequently, additional collections have been reported upon from its upper most tributaries. The species in the Powell River were listed by Ahlstedt and Brown (1980), those of the Clinch River by Stansbery (1973) and again by Bates and Dennis (1978). Ortmann (1925) reported on the lower Tennessee River, below Walden Gorge, to Muscle Shoals in Lauderdale and Colbert counties, Alabama, to which van der Schalie (1939) added additional notes. Ortmann (1924a) studied the unionids of Duck River, a tributary of the lower Tennessee. The Duck River unionids were restudied by Isom and Yokley (1968) and subsequently reexamined by van der Schalie (1973). The unionid fauna of the Cumberland River was studied by Wilson and Clark (1914), and that of the upper part of the river, above the Tennessee boundary, was examined again between 1947–1949 by Neel and Allen (1964) before the completion of the Wolf Creek Dam. Blankenship and Crockett (1972) listed the unionids found in the Rockcastle River from Livingston, Kentucky.

Ohioan Region. The first important summary of the Ohioan unionid fauna was made by Call (1897) in a paper on the molluscan fauna of the hydrographic basins of Indiana, in which he listed those species found in the Wabash River and its tributaries. Call's (1900) monograph of Indiana mollusks was supplemented by both Blatchley and Daniels (1903) and Daniels (1915) and was revised by Goodrich and van der Schalie (1944). Baker (1922) studied the molluscan fauna of the Big Vermilion River, a large tributary of the Wabash in Illinois. Meyer (1974) investigated the fauna of the Wabash and White rivers in Indiana, and Clark (1976) reviewed the unionid fauna, past and present, of the Wabash River drainage. The unionids of the Green River were extensively studied by Ortmann (1926) and were listed again by Clench and van der Schalie (1944). Stansbery (1965) added several formerly unreported species from the vicinity of Munfordville, Kentucky. The Kanawha (or New) River unionids were listed by Ortmann (1913: 305–308) and again by Morris and Taylor (1978). The fauna of the Monongahela, Allegheny, and upper Ohio rivers were discussed in Ortmann's (1919) elegant monograph of Pennsylvania naiades.

The unionids of the Tradewater and Salt rivers were listed by Clench and van der Schalie (1944), and Rosewater (1959) again listed the species of the Salt. Those of Floyd's Creek, a tributary of the Salt River, were listed by Taylor (1980b). The unionids of the Kentucky River were studied by Danglade (1922). Ortmann (1913: 308–310) listed those of the Licking and Big Sandy rivers.

In addition to the Wabash River, from west to east, there are three other major tributaries on the north side of the Ohio River: the Miami, Scioto and Muskingum. The Miami River is not included in Table 2 because there is no published list of its unionids. It is reasonable to assume that the fauna of the Miami River is, or was, similar to that of the Scioto and Muskingum rivers. A mimeographed list of the Scioto River species was circulated by Stansbery (1961). The species of Little Darby Creek, one of its tributaries, were listed by Stein (1965). Most of the species of the Muskingum drainage are covered by Sterki (1900, 1902) in papers on the

land and freshwater mollusca of the upper Tuscarawas Valley.

La Rocque's (1967) compilation on the unionids of Ohio contained useful information on the distribution of Ohio species. Ortmann's (1909, 1912, 1919) studies of the naiades of Pennsylvania record the unionid fauna of the upper Ohio drainage.

A number of mimeographed reports by state and federal agencies on the present reduced naiad fauna of the Ohioan region have appeared, and should be mentioned, although they did not include data required here. Williams (1969) reported on the mussel fisheries in the Tennessee, Ohio and Green rivers, Bates (1970) on the Ohio mussel fisheries, Dennis (1970) on the mussels of Pennsylvania, and Bates (1971) and Taylor (1980a) on the mussels of the West Virginia portion of the Ohio River.

St. Lawrence River System.

Lake Superior. The Lake Superior unionids were listed by Goodrich and van der Schalie (1932).

Lake Michigan. The unionids of Lake Michigan, and the tributaries on its western side in Wisconsin, were studied by Baker (1928). The Wisconsin tributaries were extensively collected during 1973–77 and reported on by Mathiak (1979), who added five new records. Van der Schalie (1961) enumerated the fauna of the Fox River in Wisconsin that flows into western Lake Michigan, and listed the species from a number of western Michigan rivers that flow into Lake Michigan on its eastern shore. Van der Schalie (1936, 1941, 1963) also listed the unionids of the St. Joseph, Grand and Muskegon rivers, on the lower Michigan Peninsula. The unionids of Lake Michigan proper were listed by Goodrich and van der Schalie (1932).

Lakes Huron and St. Clair. The unionids of these lakes were listed by Goodrich and van der Schalie (1932).

Lake Erie. The Lake Erie unionids were listed by Walker (1913), Ortmann (1924b), and by Goodrich and van der Schalie (1932). Stansbery and Stein (1962) circulated a useful mimeographed list of the unionids of the Island Region in the western part of Lake Erie. Robertson and Blakeslee (1948) listed the unionids found in the easternmost part of the Lake and of the rivers which flow into it in the Niagara Frontier Region. The naiades of the Huron River in southern Michigan, that flows into western Lake Erie, were studied by van der Schalie (1938). The fauna of the Maumee River, which also flows into western Lake Erie, were enumerated by Call (1897), and again by Wilson and Clark (1912) based on new collections. Clark (1977) listed the unionids of the St. Joseph River, a tributary of the Maumee. Strayer (1979) again listed the naiads of the St. Joseph River, as well as those of the Raisin and Huron rivers.

Lake Ontario. The Lake Ontario unionids were listed by Goodrich and van der Schalie (1932). Clarke and Berg (1959) monographed the unionids of Lake Ontario and those species found in the Finger Lakes Region, draining into the Lake on its south side.

Lake Champlain. The Lake Champlain unionids were listed by C. W. Johnson (1914).

Ottawa River. The unionids of Ottawa River, a major tributary of the St. Lawrence River, are based on the lists of Latchford (1882) and Whiteaves (1895), and especially on La Rocque and Oughton's (1937) account of the Unionidae of Ontario.

Canadian Interior Basin. The unionid fauna of the Arctic and Hudson Bay drainages is based on the summary by Clarke (1969) and on the distributional maps in Clarke's (1973) monograph of the Canadian Interior Basin mollusks.

Pacific Coastal Region. The list of Unionacea from the Pacific Coastal Region is from Burch (1973, 1975).

Northern Atlantic Slope Region. The

list of Unionacea from the Northern Atlantic Slope is from Johnson (1970). Papers by Athearn and Clarke (1962) and Clarke and Rick (1963) were also used.

NOMENCLATURE

The nomenclature and arrangement of the species covered in this paper are essentially those of Burch (1973, 1975). Exceptions are mentioned in the notes and under the several monographed species. The species concepts and arrangement of *Plagiola* are those of Johnson (1978), as are the Atlantic Slope species (1970). The unionid species from the Canadian Interior Basin are from Clarke (1973).

Simpson, and some later authors, especially F. C. Baker, gave nomenclatorial standing to a number of ecophenotypic variants; while the names applied to these have no standing as species or subspecies in modern systematics, some still continue to appear in the literature.

Included as notes under the species in the several faunal lists are names which have been promulgated in the literature since Simpson's (1914) monographic work on the Unionacea. Not listed are the taxa introduced by the Sicilian nobleman, Marchese A. De Gregorio (1914), who redescribed many well known North American unionids with abandon. All of his taxa were synonymized by Walker (1918) and have since been forgotten.

Morrison (1969) asserted that a number of Rafinesque's taxa, previously thought unrecognizable, had priority over a number of well known ones. Since he gave no support for his assertions, Rafinesque's names are placed under their supposed synonyms.

DISTRIBUTION OF UNIONIDAE FROM THE RIVERS SOUTH OF THE MAXIMUM PLEISTOCENE GLACIATION, WHICH FLOW INTO THE MISSOURI AND OHIO RIVERS, THAT HAVE NOT EXTENDED THEIR RANGE [Table 1]

UNIONACEA OF THE MISSISSIPPIAN AND OHIOAN REGIONS WITH REFUGIA IN TRIBUTARIES OF THE MISSOURI AND OHIO RIVERS ON THEIR SOUTH SIDE [List 1]

In addition to the 72 species listed below, the fauna also includes two species from elsewhere: a. *Margaritifera falcata* from the North Pacific Coastal Region found in the Mississippian Region, and B. *Elliptio complanata* from the North Atlantic Slope Region found in the Ohioan Region.

FAMILY MARGARITIFERIDAE

1. *Cumberlandia monodonta* (Say 1829)
   Found below the Ozark Crest only in the:
   BLACK RIVER SYSTEM

   Ouachita River Drainage. *Arkansas:* Ouachita River, above Skillern's Shoals, Arkadelphia, Clark Co. (Wheeler, 1918: 121).

FAMILY UNIONIDAE

2. *Amblema plicata* (Say 1817)
   Unio peruviana Lamarck 1819; *Amblema costata* Rafinesque 1820; *Unio undulatus* Barnes 1823; *Unio rariplicata* Deshayes 1830; *Unio perplicata* Conrad 1841; *Quadrula perplicata quintardii* Cragin 1887; *Unio pilsbryi* Marsh 1891, Nautilus **5:** 1 (Little Red River, Arkansas; holotype ANSP 41589a figured by Pilsbry, 1892, Proc. Acad. Nat. Sci. Phila. **44:** 131, pl. 8, figs. 7–8; also 1892, Nautilus **6:** 1, pl. 1, figs. 7–8); *Cokeria southalli* Marshall 1916.

3. *Fusconaia ebena* (Lea 1831)
   Obliquaria pusilla Rafinesque 1820 (Morrison, 1969: 24).

4. *Fusconaia flava* (Rafinesque 1820)
   Unio rubiginosus Lea 1829; *Unio cerinus* Conrad 1838; *Unio hebetatus* Conrad 1834; *Unio rubidus* Lea 1861; *Fusconaia flava parvula* Grier 1918.

TABLE 1

DISTRIBUTION OF UNIONIDAE OF THE RIVERS SOUTH OF MAXIMUM PLEISTOCENE GLACIATION THAT FLOW INTO THE MISSOURI AND OHIO RIVERS, THAT HAVE NOT EXTENDED THEIR RANGE

	OZARKIAN REGION				CUMBERLANDIAN REGION					
	below Ozark Crest	Osage River System	Gasconade River System	Meramec River System	Tennessee River System	Duck River Drainage	Cumberland River System	Green River System	Kanawha (or New) River System	NOTES
Lampsilis brevicula (Call 1887)	X	X	X	X						(1)
Ptychobranchus occidentalis (Conrad 1836)	X			X						(1)
Cyprogenia aberti (Conrad 1850)	X			X						(1)
Fusconaia ozarkensis (Call 1887)	X		X							(1)
Fusconaia barnesiana (Lea 1838)					X	X	X			(2)
Quadrula tuberosa (Lea 1840)					X	X	X			(3)
Pleurobema oviforme (Conrad 1834)					X	X	X			(4)
Alasmidonta raveneliana (Lea 1834)					X		X			(5)
Pegias fabula (Lea 1836)					X		X			
Actinonaias pectorosa (Conrad 1834)					X	X	X			(6)
Plagiola interrupta (Rafinesque 1820)					X		X			
Plagiola arcaeformis (Lea 1831)					X		X			
Plagiola lenior (Lea 1842)					X	X	X			
Plagiola biemarginata (Lea 1857)					X		X			
Plagiola capsaeformis (Lea 1834)					X	X	X			
Plagiola florentina (Lea 1857)	X				X	X	X			
Plagiola turgidula (Lea 1858)	X				X	X	X			
Plagiola haysiana (Lea 1834)					X		X			
Plagiola stewardsoni (Lea 1852)					X		X			
Medionidus conradicus (Lea 1834)					X	X	X			(7)
Villosa taeniata (Conrad 1834)					X	X	X			(8)
Villosa trabalis (Conrad 1834)					X		X			(9)
Villosa vanuxemensis (Lea 1838)					X	X	X			
Dromus dromas (Lea 1834)					X		X			(10)
Ptychobranchus subtentum (Say 1825)					X	X	X			
Fusconaia cuneolus (Lea 1840)					X					(11)
Fusconaia edgariana (Lea 1840)					X					(12)
Quadrula intermedia (Conrad 1836)					X					
Lexingtonia dolabelloides (Lea 1840)					X	X				(13)
Lasmigonia holstonia (Lea 1838)					X	X				(14)
Lampsilis virescens (Lea 1858)					X					(15)
Lemiox rimosus (Rafinesque 1831)					X	X				
Carunculina cylindrella (Lea 1868)					X					(16)
Pleurobema gibberum (Lea 1838)							X			(17)
Villosa ortmanni (Walker 1925)								X		(18)
Lasmigona subviridis (Conrad 1835)									X	(19)
	6	1	2	3	29	15	22	1	1	

NOTES

(1) These four species are part of the Ozarkian fauna.

(2) *Fusconaia barnesiana* (Lea 1838). Ortmann (1918: 536, 537) recognized two additional forms: *bigbyensis* (Lea 1841) and *tumescens* (Lea 1845).

(3) *Quadrula tuberosa* (Lea 1840). Not in Burch (1975). *Unio tuberosus* Lea 1840, Proc. Amer. Philos. Soc. *1*: 286 (Caney Fork [of the Cumberland River] and Cumberland River, Middle Tennessee); 1842, Trans. Amer. Philos. Soc. *8*: 210, pl. 14, fig. 25, figured holotype USNM 84219; 1842, Obs. Unio *3*: 48. Ortmann (1918: 540) regarded *Unio intermedius* Conrad 1834 (Tennessee River system), as being

the same as *Unio tuberosus* Lea 1840 (Cumberland River system), and *Unio sparsus* Lea 1841 (Tennessee River system). An examination of more recently collected material indicates that while *sparsus* is a synonym of *tuberosa*, as is *Quadrula biangulata* Morrison 1942 (Tennessee River, Tuscumbia, Colbert Co., Tennessee, holotype USNM 84221 figured by Johnson (1975a: 25, pl. 3, fig. 3), *Quadrula intermedia* (Conrad 1836), is a distinct species restricted to the Tennessee River system. Stansbery (1970: 13), writing on species in the Tennessee River system, in addition to *intermedia*, recognized *Quadrula sparsa* (Lea) as valid, and mentioned that, "this form [*sparsa*] stands between *Q. metanevra* and *Q. intermedia* and merges with neither."

(4) *Pleurobema oviforme* (Conrad 1834). Ortmann (1918: 552, 524 recognized two additional forms: *argenteum* (Lea 1841) and *holstonense* (Lea 1840).

(5) *Alasmidonta raveneliana* (Lea 1834). *Alasmodon atropurpureum* Rafinesque 1831 (Morrison, 1969: 24). Ortmann (1918: 562) recognized Rafinesque's taxa, but later Ortmann and Walker (1922: 39) declared *atropurpureum* an unidentified form. A. H. Clarke (pers. comm.) regards *raveneliana*, from the upper Tennessee River system, and *atropurpureum*, from the upper Cumberland River system, as distinct species, possibly since some specimens from the latter river system show a slight rugosity on the posterior slope.

(6) *Actiononais pectorosa* (Conrad 1834). *Lampsilis sowerbyana* Frierson 1927, Check list N American naiades, p. 69 (Duck River, Tennessee; based on the figure in Sowerby, 1868, Conch. Iconica *16, Unio*, pl. 63, fig. 316, holotype [lost] *teste* Johnson, 1972, Occ. Pap. Moll. 3: 149, pl. 28, fig. 3 [from Sowerby]).

(7) *Medionidus conradicus* (Lea 1834). Ortmann (1918: 575) as *plateolus* (Rafinesque 1831). *Medionidus* was monographed (Johnson 1977, [*conradicus*] p. 165, pl. 18, figs. 1, 2).

(8) *Villosa taeniata* (Conrad 1834). *Obliquaria teneltus* Rafinesque 1820 (Morrison, 1969: 24).

(9) *Villosa trabalis* (Conrad 1834). Stansbery (1971: 18d, fig. 37) separated *trabalis*, from the upper Cumberland River system, Kentucky and *perpurpurea* (Lea 1861) (fig. 38), from the Clinch drainage of the upper Tennessee River system, Virginia and Tennessee, possibly because specimens from the latter locality sometimes have violet nacre.

(10) *Dromus dromas* (Lea 1834). Ortmann (1918: 566) recognized an additional form: *caperatus* (Lea 1845).

(11) *Fusconaia cuneolus* (Lea 1840). Ortmann (1918: 531) recognized an additional form: *appressa* (Lea 1871).

(12) *Fusconaia edgariana* (Lea 1840). Not in Burch (1975). *Non Unio cor* Conrad 1834, *teste* Ortmann (1925: 330). Ortmann (1918: 533) recognized an additional form: *analoga* Ortmann 1918. The holotype of *Fusconaia edgariana analoga* Ortmann British Museum (Nat. Hist.) 1964117 was figured by Johnson (1977b: 236, pl. 27, fig. 1).

(13) *Lexingtonia dolabelloides* (Lea 1840). Ortmann (1918: 546) recognized an additional form: *conradi* (Vannata 1915).

(14) *Lasmigona holstonia* (Lea 1838). *Alasmidon badium* Rafinesque 1831 (Morrison 1969: 23).

(15) *Lampsilis virescens* (Lea 1858). Not in Burch (1975). Figured by Stansbery (1971: 183, fig. 40).

(16) *Carunculina cylindrella* (Lea 1868). Not in Burch (1975). Ortmann (1918: 573) did not recognize this taxon, but later, Ortmann (1925: 353) accepted it as a form of *C. maestus* (Lea 1841). Included, here, on the authority of Stansbery (1971: 18e, fig. 39), and Ahlstedt and Brown (1980, pp. 41, 43).

(17) *Pleurobema gibberum* (Lea 1838). Not in Burch (1975). *Unio gibber* Lea 1838, Trans. Amer. Philos. Soc. 6: 35, pl. 10, fig. 30 (Caney Fork [of Cumberland River], Tennessee, figured holotype USNM 84544); 1838, Obs. Unio 2: 35. Apparently restricted to the type locality.

(18) *Villosa ortmanni* (Walker 1925). This species is very close to *vanuxemensis* (Lea 1838), if, indeed, it is distinct.

(19) *Lasmigona subviridis* (Conrad 1835). This is the dominant species in the Greenbrier and New rivers of the Kanawha River system, West Virginia. Ortmann (1913: 371) suggested that his species originated in this system. With this exception, its distribution is entirely on the Atlantic slope and in the St. Lawrence River system.

Additional Notes

Alasmidonta minor (Lea 1845) was recognized by Ortmann (1918: 560) as a Cumberlandian species. Ortmann (1926: 167) later declared that it was, "an absolute synonym of *A. calceolus* (Lea 1829)." See under: 24. *Alasmidonta calceolus* in List 1. *Villosa nebulosa* (Conrad 1834) was recognized by Ortmann (1924a: 42) as a Cumberlandian species. Ortmann (1926: 180) later conceded that *nebulosa* and *iris* (Lea 1829) were the same species, but mistakenly thought that Conrad's name was the earlier. See under 68. *Villosa iris* in List 1.

5. *Fusconaia subrotunda* (Lea 1831)
Unio kirtlandianus Lea 1834; *Unio lesueurianus* Lea 1840; *Unio pilaris* Lea 1840; *Unio bursapastoris* Wright 1896; *Quadrula kirtlandiana minor* Simpson 1900, lectotype USNM 150155, selected by Johnson (1975a: 15, pl. 3, fig. 5); *Pleurobema missouriensis* Marsh 1901, Nautilus **15:** 74 (Black River, near Poplar Bluff, Missouri, holotype MZUM 38855 figured by Walker, 1915, Nautilus **28:** 140, pl. 5, figs. 1–2). Walker also determined that the shell was an ecophenotype of *subrotunda,* which occurs only in the Cumberlandian and Ohioan regions; *Fusconaja* [sic] *subrotunda leucogona* Ortmann 1913, lectotype CM 61.5239 selected by Johnson (1977: 238, pl. 27, fig. 2). *Fusconaia maculata maculata* (Rafinesque 1820). So listed by Taylor (1980a) on the authority of Stansbery who, apparently by some undisclosed means, has been able to identify *Elliptio nigra maculata* Rafinesque as *Fusconaia subrotunda* (Lea).

6. *Fusconaia undata* (Barnes 1823)
Obliquaria lateralis Rafinesque 1820 (Morrison, 1969: 24); *Unio trigonus* Lea 1831; *Unio friersoni* B. H. Wright 1896, Nautilus **9:** 134, pl. 3 (Bayou Pierre, an arm of the Red River, in De Soto Parish, Louisiana. "The type locality has been drained," *teste* Frierson, 1927, Check list N American naiades, p. 54. Lectotype USNM 133432 selected by Johnson, 1967, Occ. Papers on Moll. **3:** 6, pl. 5, fig. 4); *Unio askewi* Marsh 1896, Nautilus **10:** 91, pl. 1, figs. 3, 4 (Village Creek, Hardin Co.; Sabine River; *both* Texas. Figured holotype ANSP 70448a from the latter locality). Placed with *undata* by Ortmann (1914, Nautilus **28:** 20); *Fusconaia selecta* Wheeler, 1914, Nautilus **28:** 76, pl. 4 (Cache River, Nemo, Craighead Co., Arkansas; holotype [retained by Wheeler, possibly now in the Alabama Mus. Nat. Hist.]; paratypes MZUM 38300); *Fusconaia undata trigonoides* 'Frierson' Utterback 1915; *Fusconaia undata wagneri* Baker 1928.

7. *Quadrula cylindrica* (Say 1817)
Unio strigillatus Wright 1898. Known from the Cumberlandian and Ohioan regions, and from the Ozarkian Region below the Ozark Crest.

Specimens Examined

Ozarkian Region

Black River System

Ouachita River Drainage. *Arkansas:* Ouachita River, 3 mi. SE Pencil Bluff, Montgomery Co.; Ouachita River, Arkadelphia Clark Co.; (*both* MCZ).

Saline River Drainage. *Arkansas:* Saline River, Benton, Saline Co. (MCZ, CM).

Arkansas River System

Fall River Drainage. *Kansas:* Fall River, Wilson Co. (MCZ).

Verdigris River Drainage. *Kansas:* Verdigris River, Neodesha, Wilson Co. (MCZ).

Neosho River Drainage. *Kansas:* Neosho River, 3 mi. E Oswego, Labette Co. (Murray and Leonard); Neosho River, near state line (CM). *Oklahoma:* Neosho River, Miami, Ottawa Co. (CM).

Spring River Drainage. *Missouri:* Spring River, Carthage (MCZ); Center Creek, Webb City (CM); *both* Jasper Co.

White River System

White River Drainage. *Missouri:* White River, Hollister, Taney Co. (Utterback). *Arkansas:* White River, Cotter (MCZ, CM); North Fork White River, Norfolk (CM); *both* Baxter Co.

Big Buffalo Fork Drainage. *Arkansas:* Big Buffalo Fork, Newton, Sear-

cy, and Marion Cos. (*all* Meek and Clark).

Black River Drainage. *Missouri:* Black River, Williamsville, Wayne Co. (MCZ). *Arkansas:* Black River, Pocahontas, Randolph Co. (MCZ); Black River, Black Rock, Lawrence Co. (MCZ, CM).

Spring River Drainage. *Arkansas:* Spring River, Ravenden (Murray and Leonard); Spring River, Black Rock (MCZ); *both* Lawrence Co.

St. Francis River System

St. Francis River Drainage. *Missouri:* St. Francis River, Greenville, Wayne Co. (Utterback).

8. *Quadrula metanevra* (Rafinesque 1820)
Unio wardii Lea 1861.

9. *Quadrula nodulata* (Rafinesque 1820)
Unio pustulatus Lea 1831.

10. *Quadrula pustulosa* (Lea 1831)
Obliquaria bullata Rafinesque 1820 (Morrison 1969: 24); *Unio schoolcraftensis* Lea 1834; *Unio kieneri-anus* Lea 1852; *Unio asperatus* Lea 1861; *Unio refulgens* Lea 1868.

11. *Quadrula quadrula* (Rafinesque 1820)
Studied by Neel (1941) who included as synonyms: *Unio rugosus* Barnes 1823; *Unio lachrymosus* Lea 1828; *Unio asperrimus* Lea 1831; *Unio fragosus* Conrad 1836. Also included here as synonyms are *Unio asper* Lea 1831; *Unio prasinus* Conrad 1834; *Unio nobilis* Conrad 1854; *Quadrula quadrula contrayensis* Utterback 1915; *Quadrula quadrula bullocki* Baker 1928.

12. *Tritogonia verrucosa* (Rafinesque 1820)
Unio tuberculatus Barnes 1823.

13. *Megalonaias gigantea* (Barnes 1823)
Elliptio nervosa Rafinesque 1820 (Morrison 1969: 24); *Unio heros* Say 1829.

14. *Cyclonaias tuberculata* (Rafinesque 1820)
Unio graniferus Lea 1838; *Quadrula granifera pusilla* Simpson 1900, lectotype MCZ 20176, selected by Johnson (1966: 131, pl. 2, fig. 4); *Quadrula tuberculata utterback-iana* Frierson 1927.

15. *Elliptio crassidens crassidens* (Lamarck 1819)
Elliptio nigra Rafinesque 1820.

16. *Elliptio dilatata* Rafinesque 1820
Unio gibbosus Barnes 1823; *Unio subgibbosus* Lea 1837; *Unio gibbosus delicatus* Simpson 1900; *Elliptio dilatatus sterkii* Grier 1918.

17. *Hemistena lata* (Rafinesque 1820).

18. *Plethobasus cooperianus* (Lea 1834)
Obovaria striata Rafinesque 1820 (Morrison, 1969: 24).

19. *Plethobasus cyphyus* (Rafinesque 1820)
Unio aesopus Green 1827; *Unio compertus* Frierson 1911. Reported below the Ozark Crest from the Verdigris River, Coffeyville, Montgomery Co., Kansas. This record from the Arkansas River system was based on 3 specimens. The one in the R. E. Call collection is neither at Washburn University, Topeka, Kansas nor in the Museum of Comparative Zoology. The single valve, thought to be extant, figured by Murray and Leonard (1962: pl. 4), was sent to the National Museum of Natural History (Leonard, pers. comm., 1979), but it is not there now (Clarke, pers. comm., 1979). Branson (1967: 282) reported *P. cyphyus* from 3 localities in the Spring River of the Neosho River drainage of the Arkansas River system. These specimens could not be located at the Pittsburg [Kansas] State University (Kelting and Branson, pers. comms., 1979).

20. *Plethobasus cicatricosus* (Say 1829)
Obovaria pachosteus Rafinesque

1820 (Morrison, 1969: 24); Not in Burch (1975). See: Simpson (1914, **2:** 807), figured by Stansbery (1971, fig. 24).

21. *Pleurobema clava* (Lamarck 1819)
Not found on either side of the Ozark Crest. The several records from the Mississippian Region could not be verified, and are probably spurious. This is an Ohioan species.

22. *Pleurobema cordatum* (Rafinesque 1820)
Stansbery (1967) sent 2 pages of mimeographed ephemera on the *Pleurobema cordatum* complex to interested parties. Since he later (1970: 21) included this work in his bibliography, it is essentially quoted and discussed as if it were validly published, with additional comments in brackets. He recognized 4 species, one possibly undescribed.

(1). *Pleurobema cordatum* (Rafinesque 1820). Outline: equilateral triangle.
Unio obliqua Lamarck 1819. Unidentifiable [=*cordatum* Rafinesque (Morrison, 1969: 24). Johnson (1969, Nautilus **83:** 54) substantiated Stansbery's opinion that *obliqua* is unrecognizable].
Obovaria cordata Rafinesque 1820
Unio plenum Lea 1840. Specimen with shortened posterior [is *Pleurobema premorsa* Rafinesque 1831 (Morrison, 1969: 24)].

(2). *Pleurobema coccineum* (Conrad 1836). Outline: subcircular.
Unio coccineus Conrad 1836. Compressed with red nacre.
Unio catillus Conrad 1836. Moderately wide specimen—medium rivers.
Unio coccineum Lea 1838. Moderately wide specimen—medium rivers.
Unio solidus Lea 1838. Very wide specimen—large rivers [is *sintoxia* (Rafinesque 1820) (Morrison, 1969: 24)].
Unio cuneus Conrad 1838 (?) A wide "dwarfed" specimen.
Unio gouldianus Ward 1839. Specimen with white nacre.
Unio fulgidus Lea 1845. Moderately wide specimen—quite young.
Quadrula coccinea paupercula Simpson 1900. Stunted "Lake Erie" specimen [Lectotype USNM 134834, selected by Johnson, 1975a; 17, pl. 3, fig. 1, non *Unio paupercula* Lea 1861, unnecessarily changed by Simpson (1914, Cat. Naiades **2:** 884) to *magnalacustris*].
Pleurobema coccineum mississippiensis Baker 1928 (in part). Very wide specimen(s) from Miss. River at Lake Pepin. [Havlik and Stansbery (1978: 11) recognized *P. coccineum* as a valid species.]

(3). *Pleurobema pyramidatum* (Lea 1834). Outline: scaline triangle.
Unio pyramidatus Lea 1834 [Is *P. obliquata* (Rafinesque 1820) (Morrison, 1969: 24)]; *Unio mytiloides* Rafinesque 1820. Conrad 1836. Actually *P. clava* (Lamarck 1819).
Unio cardiacea Guerin [1829]
Pleurobema coccineum mississippiensis Baker 1928 (in part). Well developed specimen(s) from Miss. River at Lake Pepin. [Havlik and Stansbery (1978: 11) recognized *P. rubrum* (Rafinesque 1820) = *pyramidatus* Lea 1831, possibly on the basis of Ortmann's (1918: 550) recognition of *Pleurobema obliquum rubrum* (Rafinesque) and the subsequent selection of a lectotype for it, ANSP 20237, figured by Johnson and Baker (1973: 169, pl. 3, fig. 2)].

(4). *Pleurobema* ... (undescribed). Outline: isosceles triangle.

The taxa under *cordatum* and *pyramidatum* are usually associated with specimens from large rivers, while specimens that lose their sinus and become rounded with an elongated posterior end, from smaller streams and headwaters, have been incorrectly called *P. cordatum coccineum*.

[*Pleurobema cordatum* is a species with a number of ecophenotypic forms which are not species or subspecies in the modern sense. Note: *Pleurobema missouriensis* Marsh 1901. See under no. 5, *Fusconaia subrotunda* (Lea 1831)].

23. *Uniomerus tetralasmus* (Say 1831)
Unio camptodon Say 1832; *Unio sayi* Ward 1839. For the complete synonymy see: Johnson (1970: 339).

White River System

White River Drainage. *Arkansas:* Cache River, Nemo, Craighead Co. (Wheeler, 1914, Nautilus **28:** 76).

Previously unreported from the Tennessee River system. Found in Kentucky Lake, Little Eagle Creek embayment, Benton Co. in 1971 and Hurricane Creek, Henderson and Hardin Cos. in 1977; *both* Tennessee (Brown and Pardue, in press). Like *Arcidens confragosus,* no. 32, it is suggested here that *tetralasmus* was accidentally introduced behind the impoundment with fishes.

24. *Alasmidonta calceolus* (Lea 1830)
Anodonta viridis Rafinesque 1820 (Morrison, 1969: 23); *Margaritana minor* Lea 1845; *Alasmidonta calceolus danielsi* Baker 1928; *Alasmidonta calceolus magnalacustris* Baker 1928.

25. *Alasmidonta marginata* Say 1819
Margaritana marginata truncata Wright 1898; *Alasmidonta marginata variabilis* Baker 1928.

26. *Anodonta grandis grandis* Say 1829
Anodonta plana Lea 1834; *Anodonta stewartiana* Lea 1834; *Anodonta gigantea* Lea 1838; *Anodonta footiana* Lea 1840; *Anodonta virens* Lea 1852; *Anodonta opacea* Lea 1856; *Anodonta leonensis* Lea 1857; *Anodonta danielsii* Lea 1858; *Anodonta texasensis* Lea 1859; *Anodonta bealii* Lea 1863; *Anodonta dakota* Frierson 1910.

27. *Anodonta corpulenta* Cooper 1834
Regarded as a subspecies by Burch (1973: 17; 1975: 15) and Havlik and Stansbery (1978: 15). *A. corpulenta* has not been regarded as a subspecies in the modern sense, as a geographically isolated population. It is either a synonym of *grandis,* or more probably, it is a valid species.
Found in the Meramec Basin, Missouri. (Buchanan, pers. comm.).

28. *Anodonta imbecillis* Say 1829
Anodonta ohiensis Rafinesque 1820 [of authors]; *Utterbackia imbecillis fusca* Baker 1928. In spite of the statements by various authors, the original orthography is with the double "l".
Range extension on the North Atlantic Slope:

Delaware River System

Schuylkill River Drainage. *Pennsylvania:* Pickering Creek, Chester Co. (Fuller and Hartenstine, 1980). [most probably a recent introduction].

29. *Anodonta suborbiculata* Say 1831
See under species monographed.

30. *Anodontoides ferussacianus* (Lea 1834)
Anodonta subcylindracea Lea 1838; *Anodonta modesta* Lea 1857; *Anodontoides bergei* Baker 1928.

Meramec River System

Bourbeuse River Drainage. *Missouri*: Dry Fork Creek [Maries and Gasconade Cos.]; Brush Creek [Gasconade and Crawford Cos.]; (*both* Ohio State Museum, *teste*, Buchanan, pers. comm.).

White River System

Little Red River Drainage. *Arkansas*: Little Red River, Clinton, Van Buren Co. (E. Pleas, MZUM, *teste* Gordon, pers. comm.) Listed by Gordon, *et al.* (1980: 35).

St. Francis River System

St. Francis River Drainage. *Arkansas*: St. Francis River, Marked Tree, Poinsett Co. (M. Ellis, MZUM, *teste* Gordon, pers. comm.) Listed by Gordon, *et. al.* (1980: 35).

31. *Arcidens confragosus* (Say 1829)
Previously unreported from the Tennessee River system. Found in: Kentucky Lake, 6 mi. above New Johnsonville, Benton Co., Tennessee, collected in 1967 by Stansbery and Jenkinson. It is suggested that it was accidentally introduced behind the impoundment with fishes. See under species monographed.

32. *Lasmigona complanata* (Barnes 1823)
Unio katherinae Lea 1838
Previously unreported from the Ozarkian Region below the Ozark Crest.

White River System

Black River Drainage. *Missouri:* Black River, Hendrickson, Butler Co. (MCZ 260973).

33. *Lasmigona compressa* (Lea 1829)
Not found on either side of the Ozark Crest.
Not found in the Illinois River, proper, but recorded from its tributaries. *Illinois:* Vermilion River; Panther Creek, Woodford Co. (*both* Parmalee, 1967: 53, pl. 17, A).

34. *Lasmigona costata* (Rafinesque 1820)
Lasmigona costata pepinensis Baker 1928; *Lasmigona costata nuda* Baker 1928.

35. *Simpsoniconcha ambigua* (Say 1825)

White River System

Little Red River Drainage. *Arkansas:* Little Red River, Clinton, Van Buren Co. (E. Pleas, USNM, *teste*, Gordon, pers. comm.). Listed by Gordon, *et al.* (1980: 35).

Meramec River System

Bourbeuse River Drainage. *Missouri:* Bourbeuse River, 0.1 mi. S. Tea (Buchanan, Ohio State Museum). Buchanan allowed the author to examine an authentic specimen from this lot.

St. Lawrence River System

Great Lakes Drainage (Lake Michigan). *Wisconsin:* Wolf River, Shawanao Co. (Mathiak, 1979, p. 62, pl. 9, A, single specimen).

36. *Strophitus undulatus* (Say 1817)
Anodon rugosus Swainson 1822; *Alasmidonta edentula* Say 1829; *Anodonta parvonia* Lea 1836; *Strophitus undulatus tennesseensis* Frierson 1927; *Strophitus undulatus ovatus* Frierson 1927; *Strophitus rugosus pepinensis* Baker 1928; *Strophitus rugosus winnebagoensis* Baker 1928; *Strophitus rugosus lacustris* Baker 1928.

37. *Actinonaias ligamentina* (Lamarck 1819)
Unio carinatus Barnes 1823, *teste* Morrison (1969: 24). Lamarck's holotype of *Unio ligamentina* was figured by Johnson (1969, Nautilus **83:** 53; fig. 8); *Lampsilis ligamentinus*

gibbus Simpson 1900, figured holotype British Museum (Nat. Hist.) 107.10.28.262; *Lampsilis ligamentinus nigrescens* Simpson 1914, lectotype USNM 150410, selected by Johnson (1975a: 13, pl. 1, fig. 2); *Actinonaias carinata orbis* Morrison 1942, holotype USNM 85998, figured by Johnson (1975a: 32, pl. 1, fig. 3).

38. *Actinonaias ellipsiformis* (Conrad 1836)
Unio venustus Lea 1838; *Unio pleasi* Marsh 1891, Nautilus **5:** 2 (Little Red River, Arkansas, lectotype ANSP 56480a selected by Johnson and Baker, 1973, Proc. Acad. Nat. Sci. Phila. **125:** 166, pl. 9, fig. 5). Found in the streams of the southern half of the Lower Michigan Peninsula which flow into Lake Michigan. During periods of confluence, it entered the Saginaw River drainage, but it has not migrated into any of the streams of southeastern Michigan draining into Lake St. Clair or Lake Erie (van der Schalie, H. and A., 1963: 9).

39. *Carunculina parva* (Barnes 1823)
Unio texasensis Lea 1859; *Unio cromwelli* Lea 1865; *Carunculina parva calni* Baker 1927.

40. *Carunculina glans* (Lea Dec. 1831)
Toxolasma livida Rafinesque 1831 (Morrison, 1969: 24). Not in Burch (1975). See: Simpson (1914, **1:** 153). Stansbery (1970): 18) recognized *moaesta* (Lea) as a form or subspecies, which "exists in . . . several headwater streams of the Cumberland Plateau and the Southern Appalachians." Reported by Call (1885a: 31) as from the Green and Kentucky rivers, based on MCZ 5410, two specimens, so labeled. These are regarded here as erroneous records. Known from the Cumberlandian and Ohioan regions, and from the Ozarkian Region below the Ozark Crest.

Specimens Examined

Ozarkian Region

Black River System

Ouachita River Drainage. *Arkansas:* Caddo River, near Arkadelphia; Ouachita River and Old River, near Arkadelphia; Terra Noire Creek, Mt. Zion; *all* Clark Co. (*all* Wheeler, 1918: 119).

Arkansas River System

Spring River Drainage. *Missouri:* Spring River, Carthage, Jasper Co. (MCZ).

Elk River Drainage. *Missouri:* Elk River, [McDonald Co.] (Utterback).

White River System

White River Drainage. *Arkansas:* White River, Carroll Co.; James Fork of White River, Galena, Stone Co.; (*both* MCZ).

Big Buffalo Fork Drainage. *Arkansas:* Big Buffalo Fork, Searcy Co. (Meek and Clark).

Little Red River Drainage. *Arkansas:* Little Red River (MCZ).

41. *Plagiola triquetra* (Rafinesque 1820)
Found below the Ozark Crest only in the

White River System

Black River Drainage. *Missouri:* [Black River]. Poplar Bluff, [Butler Co.], (MZUM). Based on a single specimen, the locality written on the shell, with the additional data [W. A.] Marsh, March 3, 1891. This record may be spurious as is that of *Pleurobema missouriensis* Marsh 1901. See also under: no. 5. *Fusconaia subrotunda* (Lea 1831). *P. triquetra* was not listed from the Kentucky River system by Johnson (1978). Now recorded from: South Fork Kentucky River, Booneville, Ousley Co.,

Kentucky (MCZ). Found in the Muskegon, Grand and St. Joseph rivers on the eastern side of Lake Michigan, but not in the Lake proper (Johnson, 1978: 292).

42. *Plagiola torulosa* (Rafinesque 1820)
Found in the Grand River on the eastern side of Lake Michigan, but not in the Lake proper (Johnson, 1978: 296).

43. *Plagiola sampsoni* (Lea 1861)
See: (Johnson, 1978, pl. 6, fig. B, triangles).

44. *Plagiola propinqua* (Lea 1857)
See: (Johnson 1978, pl. 6, fig. B, dots).

45. *Plagiola personata* (Say 1829)
See: (Johnson, 1978, pl. 6, fig. A).

46. *Plagiola obliquata* (Rafinesque 1820)
Unio sulcatus Lea 1829.

47. *Plagiola flexuosa* (Rafinesque 1820)
Rafinesque's records: Green, Salt, and Kentucky rivers, are spurious. See: (Johnson, 1978, pl. 5).

48. *Ellipsaria lineolata* (Rafinesque 1820)
Unio securis Lea 1829.

49. *Lampsilis teres* (Rafinesque 1820)
The availability of *teres* over *anodontoides* Lea 1834 and *fallaciosus* Smith 1899 was discussed by Johnson (1972: 244). This discussion was ignored by Morrison (1979: 61) who regarded *teres* and *anodontoides* as separate species.

50. *Lampsilis fasciola* (Rafinesque 1820)

51. *Lampsilis higginsi* (Lea 1857)
Not in Burch (1975). See under species monographed.

52. *Lampsilis abrupta* (Say 1831)
Listed by Burch (1975) as *orbiculata* (Lea 1836) non Hildreth 1828. See under species monographed.

53. *Lampsilis ovata* (Say 1817)
Lampsilis cardium Rafinesque 1820; *Unio ventricosus* Barnes 1823; *Unio occidens* Lea 1829; *Unio canadensis* Lea 1857; *Lampsilis ventricosa lurida* Simpson 1914; *Lampsilis ventricosa perglobosa* Baker 1928; *Lampsilis ventricosa winnebagoensis* Baker 1928. *L. ventricosa* Barnes is regarded as a valid species by Havlik and Stansbery (1978: 11). For a discussion of ecophenotypic variation in *L. ovata* see: Johnson (1970: 388).

54. *Lampsilis radiata siliquoidea* (Barnes 1823)
Unio luteola Lamarck 1819 (Morrison, 1969: 24); *Unio rosacea* DeKay 1843; *Unio superiorensis* Marsh 1897; *Lampsilis siliquoidea pepinensis* Baker 1927; *Lampsilis siliquoidea chadwicki* Baker 1928. Johnson (1969, Nautilus **83:** 54, fig. 11) figured the type of *Unio luteola* and restricted the type locality to the Susquehanna River, Columbia, York Co., Pennsylvania. This choice from the two localities given by Lamarck, placed the equivocal type in the Atlantic Slope Region where only the typical form is found. See: Clarke and Berg (1959: 60; 80) who define *siliquoidea* as a subspecies in the modern sense. *L. radiata siliquoidea* has never been reported from the Tennessee or Cumberland River systems.

55. *Leptodea fragilis* (Rafinesque 1820)
Lampsilis simpsoni Ferriss 1900, Nautilus **14:** 38, fig. (Spring River, Hardy [Sharp Co.], Arkansas, figured holotype Field Mus. Nat. Hist. [not seen]); such specimens, without a dorsal "wing" are found throughout the range of *L. fragilis*; *Leptodea fragilis lacustris* Baker 1922.

56. *Leptodea laevissima* (Lea 1829)
Potamilus ohiensis (Rafinesque 1820) (Morrison, 1969: 24). Originally described as *Anodonta ohiensis* (*Lastena ohiensis*).

57. *Leptodea leptodon* (Rafinesque 1820)
Lampsilis blatchleyi Daniels 1902, Nautilus **16:** 13, pl. 2 (Wabash River, Section 32, Lynn Township, Posey Co., Indiana; holotype MZUM 82660). Known only from the type lot. It was suggested by Goodrich and van der Schalie (1944: 317) to be a form of *leptodon*.

58. *Ligumia recta* (Lamarck 1819)
Elliptio latissima Rafinesque 1820; *Unio sageri* Conrad 1831.

59. *Ligumia subrostrata* (Say 1831)
Lampsilis subrostrata furva Simpson 1914, lectotype USNM 126921, selected by Johnson (1975a: 13, pl. 1, figs. 4, 6).

60. *Obovaria olivaria* (Rafinesque 1820)
Unio ellipsis Lea 1828.

61. *Obovaria retusa* (Lamarck 1819)

62. *Obovaria subrotunda* (Rafinesque 1820)
Elliptio levigata Rafinesque 1820; *Unio lens* Lea 1831; *Obovaria lens parva* Simpson 1914, lectotype USNM 150457 selected by Johnson (1975a: 16, pl. 1, fig. 8); *Obovaria lens elongata* Simpson 1914, lectotype USNM 35734, selected by Johnson (1975a: 12, pl. 1, fig. 9; *Quadrula subrotunda globula* Morrison 1942, holotype USNM 85789, figured by Johnson (1975a: 29, pl. 1, fig. 7).

63. *Proptera alata* (Say 1817)
Metaptera megaptera Rafinesque 1820. Found below the Ozark Crest only in the Neosho River drainage of the Arkansas River system. (Scammon, 1906: 300; Murray and Leonard, 1962: 129).

64. *Proptera capax* (Green 1832)
Published records from the Arkansas River system are in error. See under species monographed.

65. *Truncilla truncata* Rafinesque 1820
Non *Unio truncatus* Spengler 1793; *Unio elegans* Lea 1831; *Truncilla truncata lacustris* Baker 1928.

66. *Truncilla donaciformis* (Lea 1828)

67. *Villosa fabilis* (Lea 1831)

68. *Villosa iris* (Lea 1829)
Unio nebulosus Conrad 1834, the records under this name from the Cumberlandian Region are *iris*. The type locality of *nebulosus* is: Black Warrior River [Mobile-Alabama-Coosa River system], Alabama, and it may be a valid species; *Unio ellipsiformis* Conrad 1836; *Unio novieboraci* Lea 1838.

69. *Villosa lienosa* (Conrad 1834)
Range extended into Ohio and West Virginia. Based on records in Jenkinson and Kokai (1978).

70. *Cyprogenia stegaria* (Rafinesque 1820)
See under species monographed.

71. *Obliquaria reflexa* Rafinesque 1820

72. *Ptychobranchus fasciolare* (Rafinesque 1820)
Not found in the Mississippian Region. Valentine and Stansbery (1971: 23) claim that there are specimens of this species in the Ohio State Museum from Missouri. These are probably *P. occidentalis* (Conrad).

UNIONIDAE OF THE OZARKIAN REGION WITH DISTRIBUTIONS NOT EXTENDING INTO THE MISSISSIPPIAN OR OHIOAN REGIONS [List 2]

I. *Fusconaia ozarkensis* (Call 1888)
Not in Burch (1975).
See under species monographed.

II. *Plectomerus dombeyanus* (Valenciennes 1827)
Unio trapezoides Lea 1831.

III. *Quadrula apiculata* (Say 1829)
Not in Burch (1975). Studied by Neel (1941: 4, pl. 1, figs. 5–12) who regarded *apiculata* as a subspecies of *Quadrula quadrula*.

They appear to be separate species with an overlapping distribution in the Gulf Coastal Region.

IV. *Arkansia wheeleri* Ortmann and Walker 1912
See under species monographed.

V. *Actinonaias rafinesqueana* (Frierson 1927)
Not in Burch (1975).
See under species monographed.

VI. *Plagiola florentina* (Lea 1857)
Truncilla curtisii Frierson and Utterback 1916, Amer. Mid. Nat. **4:** 453 [190], pl. 6, figs. 14 a–d, pl. 28, figs. 109 A–D (White River, Hollister, [Taney Co.], Missouri, lectotype MZUM 90748, selected by Johnson, 1978, Bull. Mus. Comp. Zool. **148:** 272, pl. 13, fig. 10).
See: (Johnson, 1978, pl. 2, dots).

VII. *Plagiola turgidula* (Lea 1858)
Truncilla lefevrei Utterback 1916, Amer. Mid. Nat. **4:** 455 [192], pl. 6, figs. 13 a–d, pl. 28, figs. 108 A–D (Black River, Williamsville, [Wayne Co.], Missouri, figured syntypes [lost]).
See: (Johnson, 1978, pl. 2, triangles).

VIII. *Glebula rotundata* (Lamarck 1819)
Unio suborbiculata Lamarck 1819.

IX. *Lampsilis excavata* (Lea 1857) Plate 15, figures 1, 2.
Several lots collected in the Black River system by the joint Harvard-Ohio State Museum expedition, 1964, confirmed the authenticity of older records from the Saline River, Benton, Saline Co., Arkansas.

X. *Lampsilis satur* (Lea 1852) Plate 14, figures 1, 2.
Unio satur Lea 1852, Trans. Amer. Philos. Soc. **10:** 205, pl. 17, fig. 19 ([Red River], Alexandria, [Rapides Parish], Louisiana; holotype USNM 84505); 1852, Obs. Unio **5:** 21.
Lampsilis ventricosa satur (Lea). Simpson, 1900, Proc. U. S. Natl. Mus. **22:** 527; 1914, Cat. Naiades **1:** 41.
Not in Burch (1975). Ortmann (1916, Nautilus **30:** 56) correctly suspected that *satur* was a valid species, distinct from *Lampsilis ovata* (Say). They occur together in the White and St. Francis river systems, but *ovata* is missing further south.

XI. *Lampsilis hydiana* (Lea 1838) Plate 15, figures 5–7.
Unio hydianus Lea 1838, Trans. Amer. Philos. Soc. **6:** 14, pl. 6, fig. 14 (Teche River, [St. Landry Parish], holotype USNM 85010; vicinity of New Orleans [Orleans Parish]; *both* Louisiana); 1838, Obs. Unio **2:** 14.
Unio placitus Lea 1852, Trans. Amer. Philos. Soc. **10:** 279, pl. 23, fig. 38 (Alabama; holotype USNM 85152) 1852, Obs. Unio **5:** 35.
Lampsilis hydiana (Lea). Simpson, 1900, Proc. U.S. Natl. Mus. **22:** 536; Cat. Naiades **1:** 66.
Simpson correctly regarded *hydiana* as a valid species distinct from *Lampsilis radiata siliquoidea* (Barnes), pointing out that *hydiana* has a more inflated shell, a more waxy texture, and that the rays are bolder, more distinct, and more brilliant. Both species occur together in the upper Arkansas, White, and St. Francis river systems, but *siliquoidea* is missing further south.

XII. *Lampsilis powelli* (Lea 1852)
Not in Burch (1975).
See under species monographed.

XIII. *Obovaria jacksoniana* (Frierson 1912)
As pointed out by Stansbery (1976: 47) *Unio castaneus* Lea December 1831 is preoccupied by *Unio castaneus* Rafinesque 1831.

XIV. *Proptera purpurata* (Lamarck 1819).

XV. *Villosa arkansasensis* (Lea 1862)
Not in Burch (1975).
See under species monographed.

XVI. *Villosa reeviana* (Lea 1852)
See under species monographed.

XVII. *Villosa vibex* (Conrad 1834) Plate 17, figures 6–8.
The synonymy was listed by Johnson (1970: 373) with the exception of:
Lampsilis streckeri Frierson 1927, Check list N American naiades, p. 74 (Little Red River, Arkansas; holotype MZUM 91075, figured by Frierson, 1928, Nautilus **41:** 139, pl. 2, fig. 1); Strecker, 1931, Baylor Univ. Mus., Special Pub. no. 2, p. 40. *Actinonaias streckeri* Valentine and Stansbery 1972, Sterkiana, no. 42, p. 32, *non* Frierson. Is *Actinonaias rafinesqueana* (Frierson 1927).
Frierson, in the original description, mentioned that the types of *streckeri* were found together with specimens of *vibex*. An examination of the type of the former with the specimens also mentioned there as from Onion Creek [of the Colorado River system], Travis Co., Texas, MZUM 79921, as *streckeri*; indicates that the "chain-like rays, sometimes becoming a ribbon or band of cross lines," which characterize *streckeri*, occur in widely separated populations of *vibex*. It is found in most coastal river systems from the Guadeloupe River system, Texas, east and north to the Cape Fear River system, North Carolina. Ozarkian region, known only from:

White River System

Little Red River Drainage. *Arkansas:* Archies Fork, Clinton (MZUM); Little Red River, Clinton (MCZ, MZUM); *both* Van Buren Co.

XVIII. *Cyprogenia aberti* (Conrad 1850)
See under species monographed.

XIX. *Ptychobranchus occidentalis* (Conrad 1836)
See under species monographed.

UNIONACEA OF THE NORTHERN ATLANTIC SLOPE REGION NORTH OF MAXIMUM PLEISTOCENE GLACIATION [LIST 3]

FAMILY MARGARITIFERIDAE

A. *Margaritifera margaritifera* (Linnaeus 1758)
Reported from the Lower Saskatchewan River by Dall, but shown to be a spurious record by Clarke (1973: 130).

FAMILY UNIONIDAE

B. *Elliptio complanata* (Lightfoot 1786)
Also found in the St. Lawrence River system and in the Ohio River system, Tuscarawas River, New Philadelphia, Tuscarawas Co., Ohio (CM). Sterki (1900: 10) suggested that it migrated from the east to Lake Erie by canals [Erie Canal] and by the Ohio Canal to the Tuscarawas River. St. Lawrence River system, not found in Lake Erie proper, but found in the Grand River, Eagleville, Ashtabula Co., Ohio (CM) (Ortmann, 1919: 110). Found in an Indian Midden ca. 1350 A.D. on the shore of the Little Miami River, Warren Co., Ohio (Russell Barber, pers. comm.). Canadian

Interior Basin, reported from the Saskatchewan River by Dall, but shown

to be a spurious record by Clarke (1973: 130).

C. *Lasmigona subviridis* (Conrad 1835)
Ortmann (1913: 371) found this to be the dominant species in the Greenbrier and New rivers of the Kanawha River system, which extends across the divide but drains to the west, into the Ohio. Ortmann thought that it spread into the Atlantic Slope region by former stream capture. With this exception, it is found only on the Atlantic slope and in the St. Lawrence drainage. It is arbitrarily regarded as an Atlantic Slope species, since it spread from there into the St. Lawrence drainage.

D. *Alasmidonta undulata* (Say 1817)

ST. LAWRENCE RIVER SYSTEM

Lake Champlain Drainage. *Vermont:* Otter Creek, Addison Co., (D. Smith, pers. comm.).

E. *Alasmidonta varicosa* (Lamarck 1819)

F. *Alasmidonta heterodon* (Lea 1830)
This species was placed in the monotypic subgenus *Prolasmidonta* by Ortmann (1914, Nautilus **28:** 44). *Prolasmidonta* was raised to generic rank by Fuller (1977: 169), based on the same data available to Ortmann. Johnson (1970: 347) maintained the subgeneric status of *Prolasmidonta.*

G. *Anodonta cataracta cataracta* Say 1817

H. *Anodonta cataracta fragilis* Lamarck 1819
marginata of authors, non Say 1817; *brooksiana* van der Schalie 1938. The concept of *fragilis* as a subspecies is based on the work of Clarke and Rick (1963: 22). The use of this combination for certain populations of *Anodonta* in the St. Lawrence River system may be suspect. The Lake Superior population, at least, might be another geographic subspecies, *A. grandis simpsoniana* Lea.

I. *Anodonta implicata* Say 1829
Morrison (1975: 36) stated that *Mytilus fucata* Dillwyn 1817 is this species, and suggested that after a century and a half of usage, Say's name should be replaced by that of Dillwyn.

J. *Strophitus undulatus* (Say 1817)
This species is ubiquitous, and is included on the list of Unionacea found in the area north of the maximum glaciation as no. 36.

K. *Ligumia nasuta* (Say 1817)

L. *Lampsilis cariosa* (Say 1817)

M. *Lampsilis ochracea* (Say 1817)
Morrison (1975: 38) stated that *Mytilus fluviatilis* Gmelin 1791 is this species, and suggested that after a century and a half of usage, Say's name should be replaced by that of Gmelin. He also removed this species from *Lampsilis,* placing it in *Leptodea.*

N. *Lampsilis radiata radiata* (Gmelin 1791)

UNIONACEA OF THE PACIFIC COASTAL REGION [List 4]

FAMILY MARGARITIFERIDAE

a. *Margaritifera falcata* (Gould 1850)
Reported from the Madison River, Montana by Stober (1972: 343) as *Margaritifera margaritifera.*

FAMILY UNIONIDAE

b. *Gonidea angulata* (Lea 1838)

c. *Anodonta beringiana* Middendorff 1851

d. *Anodonta californiensis* Lea 1852

e. *Anodonta dejecta* Lewis 1875

f. *Anodonta kennerlyi* Lea 1860

g. *Anodonta oregonensis* Lea 1838

h. *Anodonta nuttalliana* Lea 1838
Anodonta wahlamatensis Lea 1838. The first name is chosen on the basis of the page precedence.

TABLE 2

DISTRIBUTION OF UNIONACEA IN THE MISSISSIPPIAN AND OHIOAN REGIONS

A. Unionidae of the Mississippian and Ohioan regions with possible refugia adjacent to both areas.

		MISSISSIPPIAN REGION									OHIOAN REGION													
		OZARKIAN REGION						CUMBERLANDIAN REGION																
		below Ozark Crest	Black Water River **	Osage River	Gasconade River	Meramec River	Mississippi River System	Illinois River	Tennessee River	Cumberland River	Ohio River System	Wabash River	Green River	Kanawha (or New) River	Monongahela & Allegheny Rivers	Tradewater River	Salt River	Kentucky River	Licking River	Big Sandy River	Scioto River	Muskingum River	Canadian Interior Basin
2	Amblema plicata	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
12	Tritogonia verrucosa	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	
63	Proptera alata	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X		X	+	X
10	Quadrula pustulosa	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X		X		X	+ +	
4	Fusconaia flava	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X				X	X	X
53	Lampsilis ovata	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X				X	X	X
55	Leptodea fragilis	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X				X	+	
14	Cyclonaias tuberculata	X		X	+	X	X	X	X	X	X	X	X	X	X		+	X	+			X		
58	Ligumia recta	X	X	X	X	X	X	X	X	X	X	X	X	X	X		X	X				X	X	X
26	Anodonta grandis	+	X	X	X	X	X	X	X	X	X	X	X	X	X		X	X	+			X	X	X
36	Strophitus undulatus	X	X	X	X	X	X	X	X	X	X	X	X	X	X		+	X	+			X	X	X
54	Lampsilis radiata siliquoidia	X	X	X	X	X	X	X	54	54	X	X	X	X	X		X	X	+			X	X	X
37	Actinonaias ligamentina	X		X	X	X	X	X	X	X	X	X	X	X	X		X	X	+			X	X	
16	Elliptio dilatata	X	X	X	X	X	X	X	X	X	X	X	X	X	X			X				X	+ +	
22	Pleurobema cordatum	X		X	X	X	X	X	X	X	X	X	X	X	X			X				X	X	
25	Alasmidonta marginata	X		X	+	X	X	X	X	X	X	X	X	X	X			X						
15	Elliptio crassidens crassidens	X			X	X	X	X	X	X	X	X	X	X	X			+		X		X		
8	Quadrula metanerva	X				X	X	X	X	X	X	X	X	X	X				+				X	
19	Plethobathus cyphyus	X			X	X	X	X	X	X	X	X	X	X	X							X	X	
34	Lasmigona costata	X	X	X	+	X	X	X	X	X	X	X	X	X	X	X	X	X		+		X	X	X
68	Villosa iris	X				X	X	X	X	X	X	X	X	X	X							X	X	
71	Obliquaria reflexa	X		X	X	X	X	X	X	X	X	X	X	X		X		X	+				+ +	
41	Plagiola triquitra	X				X	X	X	X	X	X	X	X	X		X		X	+			X	X	
48	Ellipsaria lineolata	X	X	X	X	X	X	X	X	X	X	X	X	X		X								
49	Lampsilis teres	X	X	X	X	X	X	X	X	X	X	X	X	X			X	X	X			X	X	
65	Truncilla truncata	X		X	X	X	X	X	X	X	X	X	X	X			+	X	+			+	X	
32	Lasmigona complanata	+	X	X		X	X	X	X	X	X	X	X	X			X	X	X			X	X	X

TABLE 2. Continued

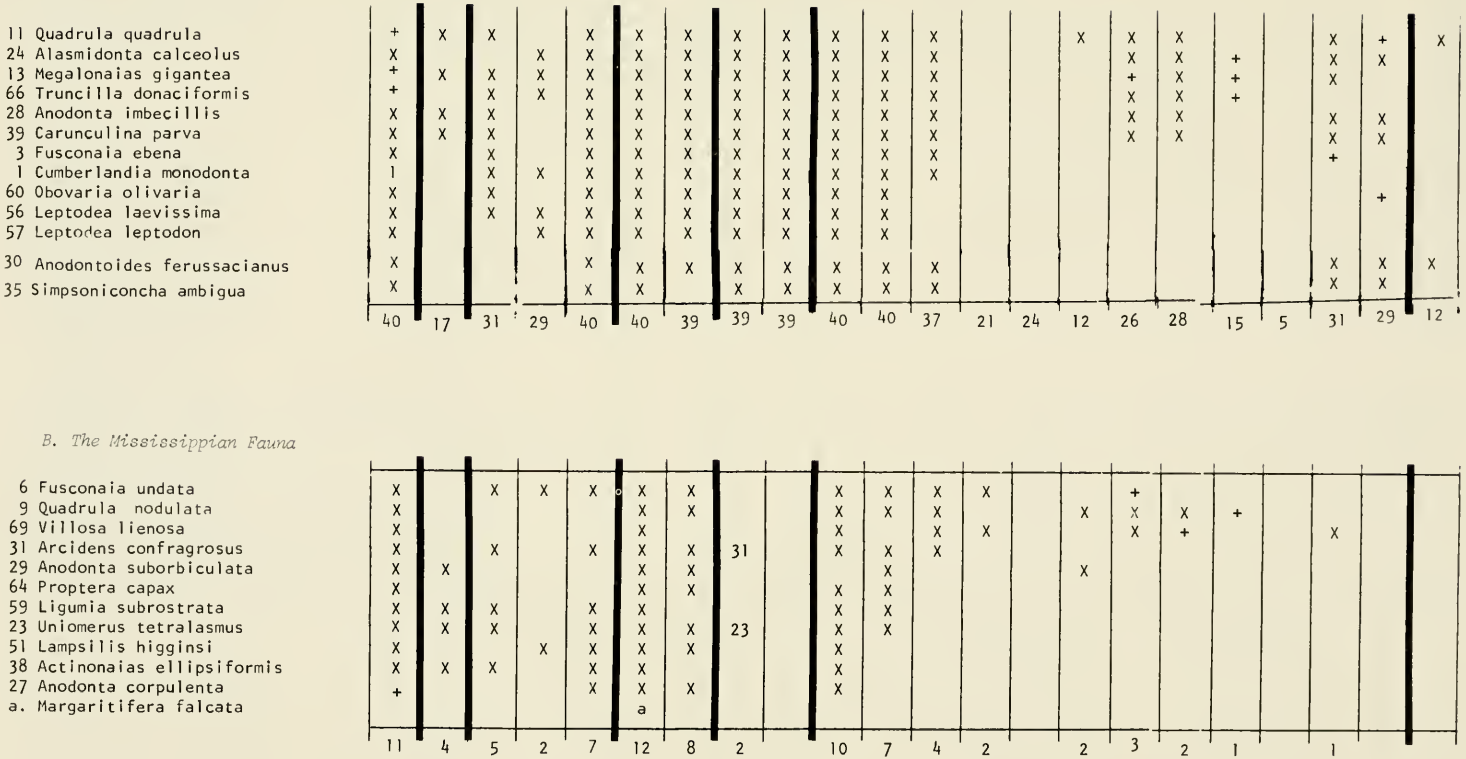


TABLE 2. Continued

C. The Ohioan Fauna

		OZARKIAN REGION				MISSISSIPPIAN REGION	CUMBERLANDIAN REGION			OHIOAN REGION												
		below Ozark Crest	Black Water River**	Osage River	Gasconade River	Meramec River	Mississippi River System	Illinois River	Tennessee River	Cumberland River	Ohio River System	Wabash River	Green River	Kanawha (or New) River	Monongahela & Allegheny Rivers	Tradewater River	Salt River	Kentucky River	Licking River	Big Sandy River	Scioto River	Muskingum River	Canadian Interior Basin
33	Lasmigona compressa						X	33	X	X	X	X			X						X	X	X
X 52	Lampsilis abrupta						X	X	X	X	X	X			X						X	X	
72	Ptychobranchus fasciolare						72		X	X	X	X	X	X	X		X	X	X		X	X	
62	Obovaris subrotunda								X	X	X	X	X	X	X		X	X		X	X	+	
21	Pleurobema clava						21		X	X	X	X	X	X	X			X			X	X	
50	Lampsilis fasciolare								X	X	X	X	X	X	X			X			X	X	
5	Fusconaia subrotunda								X	X	X	X	X	X	X					X	X	X	
70	Cyprogenia irrorata								X	X	X	X	X		X		X	X			X	X	
7	Quadrula cylindrica	X							X	X	X	X	X		X			X		X	+	X	
42	Plagiola torulosa								X		X	X	X		X			X			X	X	
67	Villosa fabilis								X		X		X	X							X	+	
17	Hemistena lata								X	X	X	X	X								X		
45	Plagiola obliquata								X	X	X	X	X						X		X		
47	Plagiola flexuosa								X	X	X	X	X					X					
18	Plethobasus cooprianus								X	X	X	X	X										
61	Obovaria retusa								X	X	X	X	X										
X 40	Carunculina glans	X							X	X	X	X											
X 20	Plethobasus cicatricosus								X	X	X	X											
X 46	Plagiola personata								X	X	X	X											
X 43	Plagiola sampsoni								X		X	X											
X 44	Plagiola propinqua								X	X	X												
8	Elliptio complanata																					X	
X Cumberlandian origin		2	0	0	0	0	1	2	20	17	21	19	14	6	10	0	3	8	2	3	13	12	2
TOTAL FROM A/B/C		53	21	36	31	47	53	48	61	56	71	66	55	29	34	14	32	38	18	8	45	41	13
TOTAL INCLUDING TABLE 1		57*		37	33	50			90	77			56	30									

*Does not include those Ozarkian species found only below the Ozark Crest

** Mississippian Region

DISTRIBUTION OF UNIONACEA IN THE MISSISSIPPIAN AND OHIOAN REGIONS [Table 2]

The number or letter preceeding the name of the species in the table refers to the designation on the several faunal lists already given.

An "X" indicates that the record was found in published works and a "+" indicates that the record is supplemental to these, based on specimens in the Museum of Comparative Zoology. A small letter, capital letter, or arabic numeral in the body of the table indicates that there are additional data in the several lists that should be consulted concerning the distribution of the species under the category in which it occurs. The rivers thought to be possible refugia for the Mississippian fauna are listed from west to east. The arrangement of the Cumberlandian and Ohioan rivers continues in the same direction but in an arbitrary fashion. The Wabash follows the Cumberlandian rivers, since these appear to be its major source of species. The Green, Kahawha, and Monongahela and Allegheny rivers then follow as the most likely refugia of some of the oldest parts of the Ohioan fauna. These are followed by other possible refugia, and then by the Scioto and Muskingum rivers which, after the Wabash, are among the major tributaries of the Ohio on its north side. As mentioned elsewhere, there is no list of the Miami River Unionidae. This river, between the Wabash and Scioto, probably has a fauna similar to that of the Scioto and Muskingum rivers.

A. Of the 74 species found in the Mississippian and Ohioan regions, with the exception of *Lampsilis radiata siliquoidea*, which is unexplainably missing from both the Tennessee and Cumberland rivers, 40 species are sufficiently ubiquitous on both sides of the Ozark Plateau, and on the Cumberland Plateau, to indicate that they may have spread into the Mississippian and Ohioan regions from either or both areas.

B. Eleven species found in both the Mississippian and Ohioan regions, mostly missing in the Tennessee and Cumberland river systems, appear to have reached the Ohioan Region from the west. Seven of these species appear to have had a refugium in the Meramec River or to have come from the Ozarkian Region south of the Ozark Crest, or from even farther south.

With the exception of *Margaritifera falcata*, of the Pacific Coastal Region, which is limited in the Mississippian Region to tributaries of the upper Missouri River in Montana, all of the species from the west are also found in the Ohioan Region. As noted by H. and A. van der Schalie (1950: 456) certain species do not usually inhabit the large rivers, but are found in smaller streams, sloughs, or lakes. Among these species are *Villosa lienosa, Anodonta suborbiculata, A. corpulenta, Ligumia subrostrata,* and *Uniomerus tetralasmus. Anodonta suborbiculata* is monographed as a representative of this group of species. *Lampsilis higginsi, Proptera capax,* and *Arcidens confragosus* are also monographed to illustrate the Ohioan penetration by several other species from the Mississippian Region.

C. The Ohioan Region has 21 species which had refugia in at least the Tennessee and Cumberland or Monongahela and Allegheny rivers. An additional species, *Elliptio complanata* from the Northern Atlantic Slope, reached the Ohioan Region by way of the St. Lawrence River system.

Only two, possibly three, of these 22 species are found in the Mississippian Region, although a number of them are found in the St. Lawrence River system. Two of these Ohioan species: *Quadrula cylindrica* and *Carunculina glans* occur in the Ozarkian Region, south of the Ozark Crest, but are entirely missing north of it. A Cumberlandian species,

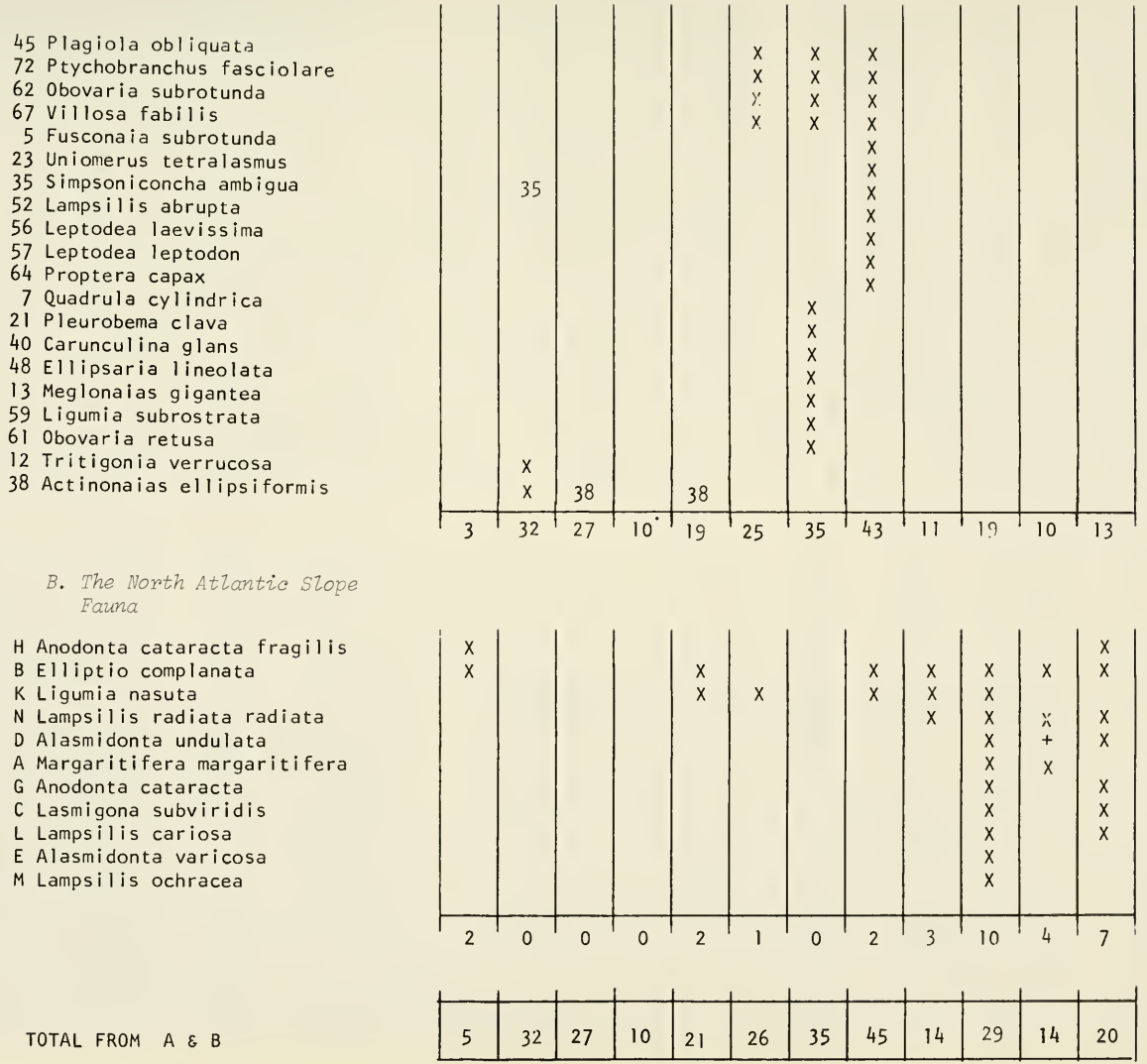
TABLE 3

DISTRIBUTION OF UNIONACEA IN THE ST. LAWRENCE RIVER SYSTEM

A. The Mississippian, Cumberlandian and Ohioan Faunas

	Lake Superior	Eastern Wisconsin Rivers	Western Michigan Rivers	Lake Michigan	Lake Huron	Lake St. Clair	Maumee River	Lake Erie	Lake Ontario	Finger Lakes Basin	Lake Champlain	Ontario River
54 Lampsilis radiata siliquoidea	x	x	x	x	x	x	x	x	x	x	x	x
26 Anodonta grandis	x	x	x	x	x	x	x	x	x	x	x	
32 Lasmigona complanata	x	x	x		x		x	x		x		x
53 Lampsilis ovata		x	x	x	x	x	x	x	x	x		x
30 Anodontoides ferussacianus		x	x	x	x	x	x	x	x	x	x	x
63 Proptera alata		x	x		x	x	x	x	x	x	x	x
58 Ligumia recta		x	x		x	x	x	x	x	x	x	x
16 Elliptio dilatata		x	x		x	x	x	x	x	x	x	x
55 Leptodea fragilis		x	x			x	x	x	x	x	x	x
25 Alasmidonta marginata		x	x		x		x	x	x	x	x	x
36 Strophitus undulatus		x	x		x		x	x	x	x	x	x
14 Cyclonaias tuberculata		x	x				x	x				
34 Lasmigona costata		x	x		x	x	x	x		x	x	x
2 Amblema plicata		x	x		x	x	x	x	x	x	x	
68 Villosa iris		x	x					x		x		
4 Fusconaia flava		x	x		x		x	x	x	x		
37 Actinonaias ligamentina		x	x			x	x	x		x		
28 Anodonta imbecillis		x	x	x	x			x		x		
39 Carunculina parva		x					x	x		x		
41 Plagiola triquetra		x	x	x		x		x				
65 Truncilla truncata		x	x	41		x		x				
22 Pleurobema cordatum		x	x		x	x	x	x				
10 Quadrula pustulosa		x	x				x	x				
71 Obliquaria reflexa		x	x			x		x				
6 Fusconaia undata		x						x				
24 Alasmidonta calceolus		x	x	x	x	x	x	x	x	x		
11 Quadrula quadrula		x	x					x				
66 Truncilla donaciformis			x			x		x				
42 Plagiola torulosa				42		x		x				
50 Lampsilis fasciola				x			x	x				
33 Lasmigona compressa		x			x	x	x	x		x	x	x
60 Obovaria olivaria		x	x		x	x	x	x		x		x

TABLE 3. Continued



Lampsilis abrupta, which also occurs in the Ohioan and Mississippian regions, is monographed.

DISTRIBUTION OF UNIONACEA IN THE ST. LAWRENCE RIVER SYSTEM [Table 3]

A. Fifty-two of the species in the St. Lawrence River system entered there from the Mississippian, Cumberlandian, and Ohioan regions.

B. Eleven species entered the St. Lawrence River system from the Northern Atlantic Slope Region.

DISTRIBUTION OF UNIONIDAE IN THE CANADIAN INTERIOR BASIN [Table 4]

Thirteen of the species found in the Hudson Bay drainage are Mississippian in origin, having entered that region from a former confluence of the Minnesota River, the upper Mississippi River and the Red River. *Lasmigona compressa*, *Lampsilis radiata siliquoidea*, and *Anodontoides ferussacianus* appear to have also invaded the Hudson Bay drainage by way of the St. Lawrence River system. *Elliptio complanata* entered only by way of the latter system. *Anodonta kennerlyi* is derived from the Pacific Coastal region. *Anodonta grandis simpsoniana* appears to be speciating within the Canadian Interior Basin. Only three unionids occur in the Arctic drainage.

DISTRIBUTION OF UNIONACEA IN THE OZARKIAN REGION [Table 5]

Fifty-three of the 74 species found in the Mississippian and Ohioan regions occur below the Ozark Crest (Plate 1, 1), and have the same arabic numerals as those in List 1. An arabic numeral in the body of the table indicates that there are additional data of general interest in the list, while one at the end of a line indicates additional data specifically on the Ozarkian Region. The uniquely Ozarkian unionacean fauna, as well as those species also found in the Gulf Coastal Region are represented by Roman numerals (List 2).

The Ozarkian rivers below the Ozark Crest are arranged on the Table from south to north, while those above the Crest are listed from east to west.

A. With the exception of *Lampsilis radiata siliquoidea*, which is missing from the Tennessee and Cumberland rivers, 40 species are found on the Ozark Plateau, above the Ozark Crest, and on the Cumberland Plateau.

B. Nine species found in the Gulf Coastal and Ozarkian regions, have extended their range into the Mississippian and Ohioan regions.

C. Nine species appear to be of southern origin.

D. Four species afford evidence of the uniformity of the fauna of the Ozarkian and Cumberland plateaus before the formation of the Mississippi River. *Quadrula cylindrica* and *Carunculina glans* are also found in the Ohioan Region, but not in the Mississippian Region.

E. With the exception of *Lampsilis higginsi* and *Proptera capax*, two Ozarkian species which have spread into the Mississippian and Ohioan regions, 8 species are unique to the Ozarkian Region.

SYSTEMATIC SECTION

Selection of the Monographed Species. Fourteen species are monographed. Eight of these are found only in the Ozarkian Region. Six others were selected to illustrate certain distributional pecularities previously discussed. The detailed distribution of the species, based on the published record, and an examination of the specimens in the major collections, is reported for the first time. Among the additional six species, are two other Ozarkian species which extended their ranges in post-glacial time, *Lampsilis higginsi* and *Proptera capax*. *Lampsilis higginsi* and *abrupta*, a closely related Cumberlandian species, are compared. They illustrate overlapping distribution in the

TABLE 4

DISTRIBUTION OF THE UNIONIDAE IN THE CANADIAN INTERIOR BASIN

		ARCTIC DRAINAGE	HUDSON BAY DRAINAGE		
		all rivers	western rivers	Red River	eastern rivers
4	Fusconaia flava (Rafinesque)			X	
11	Quadrula quadrula (Rafinesque)			X	
2	Amblema plicata (Rafinesque)			X	
34	Lasmigona costata (Rafinesque)			X	
36	Strophitus undulatus (Say)			X	
63	Proptera alata (Say)			X	
58	Ligumia recta (Lamarck)			X	
53	Lampsilis ovata (Say)			X	
26	Anodonta grandis grandis Say		X	X	X
33	Lasmigona compressa (Lea)		X	X	X
	Anodonta grandis simpsoniana Lea	X	X	X	X
54	Lampsilis radiata siliquoidea (Barnes)	X	X	X	X
32	Lasmigona complanata (Barnes)		X	X	
30	Anodontoides ferussacianus (Lea)			X	X
B	Elliptio complanata (Lightfoot)				X
f.	Anodonta kennerlyi Lea	X	X		
		3	6	14	6

Mississippian and Ohioan regions. Their specific status, nomenclature, and distribution have been matters of some dispute which are resolved here. *Cyprogenia stegaria*, a Cumberlandian species which extended its range into the Ohioan Region, is compared with *C. aberti*, an Ozarkian species. *Arcidens confragosus* and *Anodonta suborbiculata* are included as examples of species which entered the Ohioan Region from the west in postglacial time, that are widely distributed in the Gulf Coastal Region. *A. suborbiculata* was chosen to show the distribution of that group of species which do not usually inhabit the large rivers, but are usually found in smaller streams, sloughs, or lakes. Among these are also *Villosa lienosa*, *Anodonta corpulenta*, *Ligumia subrostrata* and *Uniomerus tetralasmus*.

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TABLE 5

DISTRIBUTION OF UNIONACEA IN THE OZARKIAN REGION

A. Unionacea common to both the Ozarkian and Cumberlandian Regions.

		OZARKIAN REGION									
		below Ozark Crest					above Ozark Crest				
		Red River System	Black River System	Neosho River *	White River	Black River **	St. Francis River	Meramec River	Gasconade River	Osage River	See list 1
2	Amblema plicata	X	X	X	X	X	X	X	X	X	(2)
12	Tritigonia verrucosa	X	X	X	X	X	X	X	X	X	
16	Elliptio dilatata	X	X	X	X	X	X	X	X	X	
53	Lampsilis ovata	X	X	X	X	X	X	X	X	X	
36	Strophitus undulatus	X	X	X	X	X	X	X	X	X	
71	Obliquaria reflexa	X	X	X	X	X	X	X	X	X	
65	Truncilla truncata	X	+	X	X	+	+	X	X	X	
49	Lampsilis teres	X	X	X	X	+	X	X	X	X	
55	Leptodea fragilis	X	X	X	X	+	+	X	X	X	(55)
10	Quadrula pustulosa	X	X	X	X	+	+	X	X	X	
4	Fusconaia flava	X	X	X	X	X	X	X	X	X	
11	Quadrula quadrula	X	X	X	X	+	+	X		X	
28	Anodonta imbecillis	X	X	X	+	+	+	X		X	
25	Alasmidonta marginata		X	X	+	X	X	X	+	X	
37	Actinonaias ligamentina		X	X	X	X	X	X	X	X	(37)
58	Ligumia recta		X	X	X	X	X	X	X	X	
34	Lasmigona costata		X	X	X	X	X	X	+	X	
22	Pleurobema cordatum		X	X	X	X	X	X	X	X	
3	Fusconaia ebena		+	+	X	+	+	X		X	
8	Quadrula metanerva		X	X	X	X	+	X			
14	Cyclonaias tuberculata	X		X	X	X	X	X	+	X	
54	Lampsilis radiata siliquoidea			X	X	X	X	X	X	X	
24	Alasmidonta calceolus			X	X	X	X	X	X		
48	Ellipsaria lineolata		X	X	X	+		X	X	X	
57	Leptodea leptodon		X		X	+		X	X		
60	Obovaria olivaria				X	+	+	X		X	
68	Villosa iris				X	X		X			
39	Carunculina parva	X	X	X	X		X	X		X	
15	Elliptio crassidens crassidens		+		X			X	X		
26	Anodonta grandis grandis	X	X	X	X		+	X	X	X	
66	Truncilla donaciformis	X	X	X		+	+	X	X	X	
32	Lasmigonia complanata	X	X	X		+	+	X		X	(32)
41	Plagiola triquetra					41		X			
56	Leptodea laevissima	X		X		+	+	X	X	X	
13	Megalonaias gigantea	X		X			+	X	X	X	
63	Proptera alata			X				X	X	X	(63)
19	Plethobasus cyphyus			X				X	X		(19)
1	Cumberlandia monodonta		X					X	X	X	(1)
30	Anodondoites ferussacianus				X		X	X			(30)
35	Simpsoniconcha ambigua				X			X			(35)
		20	28	32	32	31	31	40	29	31	

extended to my colleagues, Dr. Kenneth J. Boss who read the manuscript; and to Dr. Ruth D. Turner who thankfully read the manuscript with a very critical eye. Dr. Arthur H. Clarke of the National Museum of Natural History kindly read the manuscript and made a number of significant suggestions. Dr. David H. Stansbery, of the Ohio State Museum, helpfully, offered several opinions. Mr. Douglas G. Smith, of the Museum of Zoology, University of Massachusetts, Am-

TABLE 5. Continued

	OZARKIAN REGION									
	below Ozark Crest					above Ozark Crest				
	Red River System	Black River System	Neosho River *	White River	Black River **	St. Francis River	Meramec River	Gasconade River	Osage River	See list 1 or 2
B. Unionidae common to both the Gulf Coastal and Ozarkian Regions, also found in the Mississippian and Ohioan Regions.										
6 Fusconaia undata	X	X		X	+	X	X	X	X	(6)
31 Arcidens confragrosus	X			X	X	X	X		X	
23 Uniomerus tetralasmus	X	X	X	X		X	X		X	(23)
59 Ligumia subrostrata	X	X	X		+	X	X		X	
38 Actinonaias ellipsiformis			+	X	X		X		X	(38)
9 Quadrula nodulata	X	+	X	X	+	+				
69 Villosa lienosa	X	X		X	X	X				
29 Anodonta suborbiculata	+	X	X		X	X				
27 Anodonta corpulenta	X	+		X		+	X			
	8	7	5	7	7	8	6	1	5	
C. Unionidae common to both the Gulf Coastal Region and the Ozarkian Region, below the Ozark Crest.										
XIV Proptera purpurata	X	X	X	+	+	+				
XI Lampsilis hydiana	X	X		X	+	X				(X)
XIII Obovaria jacksoniana	X	X		X	+	X				
II Plectomerus dombeyanus	X	X		X	+	+				
X Lampsilis satur	X	X		X	X	+				(IX)
XVII Villosa vibex				X						
III Quadrula apiculata	X									
VIII Glebula rotundata	X									
IX Lampsilis excavata		+								(VIII)
	7	6	1	5	5	5	0	0	0	
D. Unionidae common to both the Ozarkian Region, below the Ozark Crest, and the Cumberlandian Region.										
7 Quadrula cylindrica		X	X	X	X	X				
40 Carunculina glans		X	+	X						
VI Plagiola florentina				X	X					
VII Plagiola turgidula				X	X					
	0	2	2	4	3	1	0	0	0	
E. The Ozarkian Fauna										
XIX Ptychobranchus occidentalis	X	X	X	X	X	X	X			
XVIII Cyprogenia aberti		X	X	X	X	X	X			
51 Lampsilis higginsi		X		X	X		X	X		(51)
XII Lampsilis powelli		X	X	X						
I Fusconaia ozarkensis			X	X	X	X		X		
V Actinonaias rafinesqueana			X	X	X					
XVI Villosa reeviana				X	X		X	X	X	
64 Proptera capax				X		X				
IV Arkansia wheeleri	X	X								
XV Villosa arkansasensis		X								
	2	6	5	8	5	4	4	3	1	
Total A-E	37	49	45	56	51	49	50	33	37	

* Arkansas River System
All the species are found in the Neosho River drainage.

** White River System

** Total 63

herst, supplied certain data on the Lake Champlain fauna. Most of the photographs were taken by Mr. David L. MacHenry. The maps and tables were carefully prepared by Miss Catharine G. Kessler who also helped with other numerous details, including proofreading.

At my last moment request, Steven Ahlstedt, Tennessee Valley Authority; Alan C. Buchanan, Missouri Department of Conservation; Mark E. Gordon; University of Arkansas; and R. D. Oesch, Glendale, Missouri; all kindly supplied me with data and specimens.

Pattern Used in Descriptions.

Abbreviations. The following abbreviations have been used in the text and on the plate captions:

ANSP	Academy of Natural Sciences of Philadelphia, Pennsylvania
CM	Carnegie Museum, Pittsburgh, Pennsylvania
MCZ	Museum of Comparative Zoology, Cambridge, Massachusetts
MZUM	Museum of Zoology, University of Michigan, Ann Arbor, Michigan
OSM	Ohio State Museum, Columbus, Ohio
USNM	National Museum of Natural History, Washington, D. C.

Synonymy. For ease of reference, full citations are included for each taxon, including the type locality and the location of the type when known. References to plates and figures are not included under Lea's *Observations on the Genus Unio* since they are always the same as in the preceding entry. In some instances, lectotypes are selected. Elsewhere in the text, references are abbreviated and require the use of the bibliography. Except for the original references, only relevant citations since 1914 are included here since earlier ones are available in Simpson (1914).

Descriptions. The measurements are only intended to convey the general size of specimens from a given station, and to indicate sexual differences.

Anatomy and Breeding Season. The available data are cited.

Habitat. Included when known.

Remarks. These are designed to elucidate the differences between the sexes and the species, and include comments on distribution and taxonomy.

Range. The distribution is summarized.

Abundance. The former abundance of the species is based on the number and size of the lots found in the several collections studied. Their present abundance is based on the opinions of Stansbery (1970, 1971, 1976).

Specimens Examined. Most of the records are based on the specimens in the collections mentioned above. These collections contain most of the specimens available for study. With the exception of those in the Ohio State Museum, most of those in the other institutions have been personally examined. The records are followed by the initials of the institution in which they were observed. In most instances when records were duplicated only references to the specimens in the Museum of Comparative Zoology were included, though in certain critical cases several references are mentioned. Specimens not seen are credited to the responsible individual or published reference and to the associated institution, if it is known. The published references may be found either under *Synonymy* or under *Literature Cited*, or sometimes under both headings.

Distribution. The various river systems are listed from west to east. East of the Mississippi River this arrangement approximates the direction of post-glacial dispersal.

Arrangement of the Records. The river systems of the Gulf Coastal Region are listed from west to east. The drainages below the Ozark Crest are listed from south to north. In the Ozarkian Region, above the Crest, the rivers flowing into the Missouri from the south are listed from west to east. The records for all of the above mentioned rivers are arranged

from the headwaters to the mouth. Above the Missouri River the Mississippian drainages are listed from south to north and the records are arranged from mouth to headwaters, approximating the direction of post-glacial dispersal. In the Cumberlandian and Ohioan regions the rivers flowing into the Ohio are listed from west to east. The records of those on the south side of the Ohio River are arranged from headwaters to mouth, while those of the Ohio itself and the tributaries above it are arranged from mouth to headwaters, approximating the direction of post-glacial dispersal.

The cumbersome term, Mobile-Alabama-Coosa river system, is used because it reflects the main channel of the river, which was given a different name at each important confluence.

Figures. When available, holotypes, allotypes and lectotypes are generally used to illustrate each species. Some of the data on the plate captions, such as the measurements, are not repeated elsewhere.

The distributional maps are based on Rand McNally and Company's *Commercial Atlas of America* 1912 Edition, plate 21, which indicates United States Inland Waterways.

Superfamily **UNIONACEA** Thiele 1935
Family UNIONIDAE (Fleming 1828) Ortmann 1911
Subfamily AMBLEMINAE
Tribe AMBLEMINI
Genus *Fusconaia* Simpson

Fusconaia Simpson 1900, Proc. U. S. Natl. Mus. **22:** 784. Type species, *Unio trigonus* Lea, original designation.

Fusconaia ozarkensis (Call)
Plate 9, figures 1–4
Distribution: Plate 8 A

Unio ozarkensis Call 1887, Proc. U. S. Natl. Mus. **10:** 498, pl. 27 (Currant [Current] River, Shannon Co., Missouri, and in Jacks Fork and Big Creek, tributaries to it; lectotype MCZ 5707 selected by Johnson, 1975, Occ. Papers on Moll. **4:** 143, specimen portrayed in figs. 1–3; figured paralectotype MCZ 5705; *both* from Jacks Fork [Shannon Co.]).

Pleurobema brevis subelliptica Simpson 1900, Proc. Acad. Nat. Sci. Phila. **52:** 80 (Spring River, Hardy [Fulton Co.], Arkansas; lectotype USNM 159952 selected by Johnson, 1975, Special Occ. Pub. no. 4, Dept. Moll., Mus. Comp. Zool., p. 20, pl. 2, fig. 7).

Pleurobema pannosa Simpson 1900, Proc. Acad. Nat. Sci. Phila. **52:** 82 (White River; [Ouachita River], Hot Springs, [Garland Co.]; *both* Arkansas); 1900, Proc. U. S. Natl. Mus. **22:** 799. The measured type, from the latter locality, was not located by Johnson (1975a: 16). Included in this synonymy on the authority of Ortmann (1917, Nautilus **31:** 62).

Pleurobema utterbackii Frierson 1915 [in] Utterback, Amer. Midl. Nat. **4:** 197 [86], pl. 5, figs. 12 a, b; pl. 20, figs. 63 A–D (White River, Hollister, [Taney Co.], Missouri; holotype MCZ 271448, refigured by Johnson, 1972, Occ. Papers on Moll. **3:** 151, pl. 24, fig. 5).

Quadrula flava sampsoniana Frierson 1927, Check list N. American naiades, p. 55 (Elk River, [McDonald Co.], Missouri; holotype MZUM 92226, refigured by Johnson, 1972, Occ. Papers on Moll. **3:** 149, pl. 25, fig. 5).

Fusconaia ozarkensis (Call). Ortmann, 1917, Nautilus **31:** 62.

Description. Shell medium in size, seldom exceeding 70 mm in length. Outline elliptical to subtrapezoid. Valves usually somewhat compressed, solid, inequilateral. Anterior end regularly rounded. Posterior end slightly biangulate below the medial line. Ventral margin straight or regularly curved. Dorsal margin straight forming an indistinct angle with the obliquely descending posterior margin. Hinge ligament long. Posterior ridge double, but very faint. Umbos small and low, not much projected above the hinge line, their sculpture consisting of several coarse undulations. Surface of the shell rather smooth, rest stops usually clearly marked. Periostracum yellowish-brown or olivaceous, often marked with numerous obscure narrow green rays, arranged on the central portion of the disk.

Left valve with two triangular pseudocardinal teeth of about equal height, two curved lateral ones. Right valve with one high, triangular pseudocardinal, a smaller one before and behind it, and one strong lateral tooth. Anterior and poste-

rior muscle scars, and pallial line all well impressed. Nacre usually white or bluish, iridescent posteriorly.

Length mm	Height mm	Width mm	
68	42	26	White River, Hollister, Taney Co., Missouri. Holo of *P. utterbackii*.
59	38	20	Big Fork, Texas Co., Missouri.
55	36	20	Jacks Fork, Shannon Co., Missouri. Lectotype of *U. ozarkensis*.

Anatomy and Breeding Season. The anatomy was discussed by Ortmann (1917: 63), and on the basis of it, he recognized that *ozarkensis* was a *Fusconaia*. He further noted that the glochidia are subelliptical, slightly higher than long; 0.15 × 0.18, and that the species is tachytictic.

Habitat. Found by Call in shallow mountain streams, "being swift, and limpid, with rocky bottoms."

Remarks. Fusconaia ozarkensis (Call) does not much resemble any other Ozarkian species. It is, however, very close to *Fusconaia barnsiana* (Lea) of the Cumberlandian Region. *F. ozarkensis* has a more elongated, subtrapezoidal shell, more anterior umbos, and the rays on the disk are faint, at best, and generally entirely wanting, where those of *barnsiana* are well developed.

Ortmann (1917: 63) indicated that the syntype, subsequently selected as the lectotype, is less typical of the general shape of the shell than is that of the figured paralectotype, and that the difference in shell morphology is not a sexual one as it was thought to be by Call.

Range. Found only in the Ozarkian Region: below the Ozark Crest in the Black, Arkansas, White, and St. Francis river systems; and above it in the Gasconade River system.

Abundance. Apparently not taken in large numbers, except in the Current River drainage of the White River system and in the Big Piney River of the Gasconade River system.

Specimens Examined

Black River System

Ouachita River Drainage. *Arkansas:* [Ouachita River] Hot Springs, Garland Co. (Simpson).

Arkansas River System

Neosho River Drainage. *Missouri:* Neosho River (Utterback, 1917, Table [as *utterbackii*]); Elk River, McDonald Co. (MZUM).

White River System

White River Drainage. *Missouri:* James River, Galena, Stone Co.; White River, Hollister, Taney Co. (*both* MCZ). *Arkansas:* White River, Cotter (MZUM), and Norfolk (CM), *both* Baxter Co.; Big Buffalo Fork of White River, below Gilbert, Searcy Co. (Meek and Clark, 1912: 10).

Current River Drainage. *Missouri:* Big Creek, Texas Co.; Jacks Fork; Current River, 5.8 mi. NE Eminence; *both* Shannon Co.; Current River 1 mi. SW Doniphan, Ripley Co. (*all* MCZ).

Spring River Drainage. *Arkansas:* Spring River, Hardy, Fulton Co. (MCZ).

St. Francis River System

St. Francis River Drainage. *Missouri:* St. Francis River (Utterback, 1917, Table [as *utterbackii*]).

Gasconade River System

Gasconade River Drainage. *Missouri:* Big Piney River, 10 mi. W Licking, Texas Co.; Gasconade River, 6 mi. NW Vichy, Maries Co. (*both* MCZ).

Subfamily UNIONINAE
Tribe ANODONTINI
Genus *Anodonta* Lamarck

Anodonta Lamarck 1799, Memoires de la Soc. d'Hist. Nat. de Paris, p. 87. Type species, *Mytilus cygneus* Linnaeus. Monotypic. Placed on the Official List of Generic Names in Zoology, in 1926, Opinion 94. Reconfirmed, 1959, Opinions and Declarations rendered by Int. Comm. Zool. Nomen., **20** (28): 303–310, Opinion 561.

Subgenus *Utterbackia* F. C. Baker

Utterbackia F. C. Baker 1927, Amer. Midl. Nat. **10:** 221, 222 (misspelled as *Utterbachia* on p. 221). Type species, *Anodonta imbecillis* Say, original designation.

Utterbackiana Frierson 1927, Check list N American naiades, p. 17. Type species, *Anodonta suborbiculata* Say, monotypic. Discussed by Johnson, 1970, Bull. Mus. Comp. Zool. **140:** 362.

Nayadina Haas 1969, Das Tierreich, pt. 88, p. 359, *non* Gregorio 1914. Walker (1918: 176) correctly pointed out that the type species of *Nayadina*, *Anodonta venusta* Gregorio is a synonym of *Anodonta grandis* Say.

Anodonta (*Utterbackia*) *suborbiculata* Say

Plate 9, figure 5
Distribution: Plate 5

Anodonta suborbiculata Say 1831 [Jan. 29] New Harmony [Indiana] Disseminator [no pagination] (Ponds near the Wabash [River, near New Harmony, Posey Co., Indiana], type ANSP [lost], *teste* Johnson and Baker, 1973, Proc. Acad. Nat. Sci. Phila. **125:** 146). Say, 1831, American Conch. no. 2 [letter press], pl. 11. Simpson, 1914, Cat. Naiades **1:** 400. Parmalee, 1967, Illinois State Mus. Pop. Sci. Ser. **8:** 48, pl. 15 B. Starrett, 1971, Illinois Nat. Hist. Surv. Bull. **30:** 320, pl. 3, fig. 19.

Anodonta (*Utterbackiana*) *suborbiculata* Say. Frierson, 1927, Check list N American naiades, p. 17.

Anodonta (*Nayadina*) *suborbiculata* Say. Haas, 1969, Das Tierreich, pt. 88, p. 360.

Description. Shell medium to large, reaching over 130 mm in length. Outline suborbiculate. Valves subinflated, thin but strong, gaping in front and behind. Anterior end regularly rounded, posterior end broadly pointed at about the medial line. Ventral margin regularly curved. Dorsal margin straight, ending in a wing like angle before and behind. Posterior slope slightly incurved above the low posterior ridge. Umbos very low and compressed in young specimens, becoming somewhat fuller in adults, but not much if at all; raised above the hinge line, umbonal sculpture consisting of a few irregular, feeble undulations, each of which has on it, small sharp, tubercles which form two imperfectly radiating rows, located somewhat anterior of the center. Periostracum smooth and shining in young shells, pale yellow green, with numerous very fine green rays. Older shells are concentrically sculptured and the periostracum is smokey or yellowish and often nearly rayless.

Hinge without any trace of denture. Umbonal cavities shallow. Muscle scars indistinct. Nacre silvery and iridescent, sometimes tinted bluish or purplish.

Length mm	Height mm	Width mm	
170	126	58	Keokuk Lake, Muscatine, Muscatine Co., Iowa.
130	100	43	Spoon River, Illinois.

Anatomy and Breeding Season. The anatomy and breeding season of *A. suborbiculata* are not known. Sexuality and other aspects of reproduction of all the other members of the subgenus *Utterbackia* are discussed by Heard (1975). A glochidium was figured by Surber (1915: 4, pl. 1, fig. 1).

Habitat. Found in a sand or mud bottom, in water with an average depth of five to eight feet, usually in lakes or sloughs where the current is not strong.

Remarks. Anodonta suborbiculata Say is very easily identified. Since the hinge teeth are completely absent it is easily recognized as an *Anodonta*, and as the umbos are flat, and not raised above the hinge line it may be recognized as belonging to the subgenus *Utterbackia.* Its orbiculate outline separates it from the other members of the subgenus.

The records of *A. suborbiculata* from Nebraska (Aughey, 1877) have never been verified. This species was not found in the Tennessee River system by Ortmann (1918, 1924, 1925) which suggests that its occurrence behind the Wheeler Dam may be the result of the subsequent introduction of fishes. In any event, the dam created an environment the species prefers.

Range. Gulf Coastal Region: Trinity River system, Texas and the Escambia River system, Florida. Lower Mississippi River drainages. Ozarkian Region: Red

and Black river systems, Arkansas; Arkansas River system, Kansas; White and St. Francis river systems, Missouri and Arkansas; all below the Ozark Crest; above it, the Meramec River system, Missouri. Mississippian Region: Missouri and Illinois rivers; Mississippi River and drainages from Illinois north to Wisconsin. Cumberlandian Region: Tennessee River, Alabama. Ohioan Region: Wabash River drainage, Indiana; Green River, Kentucky.

Abundance. This species appears to be rare, though occasionally very abundant locally. Taken in great numbers by Strode (1891) in Thompson's Lake, Illinois.

Specimens Examined

Gulf Coastal Region

Trinity River System

Trinity River Drainage. *Texas:* Wards Prairie Lake, nr. Romayor, Liberty Co. (MCZ).

Escambia River System

Escambia River Drainage. *Alabama:* Escambia River, nr. Pollard, Escambia Co. (MZUM). *Florida:* Chumucklee Spring Lake, nr. McDavid, Escambia Co. (MZUM).

Conecuh River Drainage. *Alabama:* Gantt Lake, Clearview, Covington Co. (MCZ).

Ozarkian Region

Red River System

Red River Drainage. *Arkansas:* Little River (MZUM). Mercer Bayou, N Black Diamond, Miller Co. (MCZ). *Louisiana:* Red River (MZUM); Frierson (USNM); Clear Lake; Edwards Lake (*both* MZUM); *all* De Soto Parish. Black Lake Bayou, Lebanon, Bienville Parish. [Red River] Alexandria, Rapides Parish (USNM).

Black River System

Ouachita River Drainage. *Arkansas:* Old River, Arkadelphia, Clarke Co. (Wheeler, 1918: 121).

Arkansas River System

Neosho River Drainage. *Kansas:* Neosho River, Woodson Co. (Call, 1885b: 96); pond E Neosho River, 4.5 mi S Humboldt, Allen Co. (Murray and Leonard, 1962: 160).

White River System

Black River Drainage. *Missouri:* Black River, Hendrickson, Butler Co. (MCZ). *Arkansas:* Black River, Black Rock (MCZ); Spring River, Black Rock (MZUM); *both* Lawrence Co.

St. Francis River System

Tyronza River Drainage. *Arkansas:* Pond, nr. Tyronza River, Tyronza, Poinsett Co. (MZUM).

Meramec River System

Meramec River Drainage. *Missouri:* Creve Coeur Lake, St. Louis Co. (MCZ).

Mississippi River System

Mississippi River Drainage. *Tennessee:* Mississippi River, Presidents Island, nr. Memphis, Shelby Co. (MCZ).

Mississippian Region

Missouri River System

Elkhorn River Drainage. *Nebraska:* Elkhorn River (Aughey 1877: 704).

Missouri River Drainage. *Missouri:* Lake Contrary, St. Joseph, Buchanan Co. (MZUM).

Kansas River Drainage. *Nebraska:* Big Blue River (Aughey 1877: 704).

Mississippi River System

Mississippi River Drainage. *Illinois:* Mississippi River, Alton, Madison Co. (MCZ).

Sangamon River Drainage. *Illinois:* Clear Lake nr. Springfield, Sangamon Co. (MCZ).

Spoon River Drainage. *Illinois:* Spoon River; Simpsons Lake; Thompsons Lake; (*all* MCZ) *all* Fulton Co.

Illinois River Drainage. *Illinois:* Illinois River, Mossville, Peoria Co. (Starrett, 1971: 320).

Kaskaskia River Drainage. *Illinois:* Kaskaskia River (Parmalee, 1967: 48).

Mississippi River Drainage. *Iowa:* Keokuk Lake, Muscatine, Muscatine Co. (MCZ). *Wisconsin:* Mississippi River, La Crosse, La Crosse Co. (Mathiak, 1979: 7).

Cumberlandian Region

Tennessee River System

Tennessee River Drainage. *Alabama:* Tennessee River, Wheeler Reservoir [Lawrence Co.] (MZUM).

Ohioan Region

Ohio River System

Wabash River Drainage. *Indiana:* Ponds nr. the Wabash River, New Harmony, Posey Co. (Say); Wabash River (Call, 1900: 533).

Green River Drainage. *Kentucky:* Barren River; Pond nr. Bowling Green, Warren Co. (*both* MZUM).

Genus *Arcidens* Simpson

Arcidens Simpson 1900, Proc. United States Natl. Mus. **22:** 661. Type species, *Alasmodonta confragosa* Say, original designation. This genus is monotypic.

Arcidens confragosus (Say)

Plate 10, figures 1, 2
Distribution: Plate 4

Alasmodonta confragosa Say 1829, New Harmony [Indiana] Disseminator **2** (22): 339 (Fox River, of the [Little] Wabash [River, Richland Co., Illinois], type ANSP [lost], *teste* Johnson and Baker, 1973, Proc. Acad. Nat. Sci. Phila. **125:** 146); 1831, American Conch. no. 3 [letter press], pl. 21; 1832, no. 4, p. [4] of wrapper.

Arcidens confragosa jacintoensis Strecker 1931, Baylor Univ. Mus. [Waco, Texas], Spec. Pub. 2, p. 13 (San Jacinto River, Liberty Co., Texas; syntypes presumed to be in the Strecker Museum [not available]; topotype MCZ 23317).

Arcidens confragosus (Say). Simpson, 1914, Cat. Naiades, **1:** 475. Utterback, 1915, Amer. Midl. Nat. **4:** 254 [103], pl. 22, figs. 72 A and B. Coker, 1919, Bull. U. S. Bur. Fisheries for 1917–18, **36:** 34, pl. 21, lower pair. Frierson, 1927, Check list N American naiades, p. 21. Baker, 1928, Wisconsin Geol. and Nat. Hist. Surv. Bull. **70** (2): 196, pl. 63, figs. 4–7. Murray and Leonard, 1962, Univ. Kansas, Mus. Nat. Hist. Misc. Pub. **28:** 97. Parmalee, 1967, Illinois State Mus. Pop. Sci. Ser. **8:** 51, pls. 16 A; 33 A. La Rocque, 1967, Ohio Geol. Surv. Bull. no. 62 (2): 208, fig. 94; fig. 95 distributional map. Haas, 1969, Das Tierreich, pt. 88, p. 396. Starrett, 1971, Illinois Nat. Hist. Surv. Bull. **30:** 312, pl. 3, fig. 13.

Description. Shell medium to large, often exceeding 100 mm in length. Outline rhomboid. Valves inflated, subsolid, or solid, slightly inequilateral. Anterior end regularly rounded. Posterior end somewhat produced below the medial line. Ventral margin regularly curved. Dorsal margin straight, forming a sharp wing like angle with the very straight, obliquely descending posterior margin. Hinge ligament long. Posterior ridge rather high, but indistinct. Posterior slope with numerous heavy, radial corrugations. Umbos high and full, much projected above the hinge line, their sculpture consisting of irregular, doubly-looped ridges, the bases of the loops being developed into strong, pinched-up nodules, which extend out on to the disk of the shell; in front of, and behind, the loops there are a number of radiating, wavy, subnodulous lirae or small ridges; from the anterior row of knobs extending backwards and downwards there is a series of strong folds and these are crossed by wrinkled, radiating, sometimes zigzagged threads. The anterior base usually has merely concentric striae. Periostracum subshiny or dull, brownish green, or olive; occasionally quite greenish and banded.

Left valve with an arched, somewhat elongated pseudocardinal tooth under the umbo which curves upward, in front of which, there is a lower compressed

tooth. Right valve with a strong subcompressed tooth in front of the umbo. The hinge plate is cut away from the umbo for the reception of the tooth in the left valve. The lateral teeth reduced to vestigial blurs. Umbonal cavities deep, anterior muscle scars shallow, posterior ones and pallial line quite indistinct. Nacre bluish-white or dull white, with a wide prismatic border.

Length mm	Height mm	Width mm	
115	78	48	Rough River, Dundee, Ohio Co., Kentucky.
105	77	51	Fox River, Illinois. Topotype MCZ 53004.
84	57	32	San Jacinto River, Texas. Topotype MCZ 23317.

Anatomy and Breeding Season. The anatomy was discussed by Ortmann (1912: 284, fig. 12). A glochidium was figured by Surber (1912, pl. 1, fig. 5) 0.355 × 0.350. This species is bradytictic, probably from September to June (Baker, 1928: 197). Host fish not recorded.

Habitat. Found in a sand or mud bottom in sluggish water a few feet deep.

Remarks. Arcidens confragosus (Say), a widely distributed species, is not very closely related to any other unionid, except *Arkansia wheeleri* Ortmann and Walker which is found only in the Ozarkian Region in the upper Red and Black river systems. The sculpture of *Arcidens* is much more complicated than that of *Arkansia* and covers most of the surface of the shell, while that of *Arkansia* is restricted to the posterior half of the disk. The radiating wrinkles and curved folds on the dorsal slope are much alike in both, but the folds on the posterior disk of *Arkansia* more closely resemble those of *Amblema plicata* (Say). The umbonal sculpture of *Arcidens* somewhat resembles that of *Quadrula quadrula* Rafinesque, but *Arcidens* does not much resemble the latter in any other way. While the umbonal sculpture of *Arkansia* is comparatively simple and confined to the upper umbo, that of *Arcidens* is developed into strong pitched up nodules, at the base of the loops, and extends out onto the disk. The lateral teeth in *Arcidens* are not as well developed as those of *Arkansia*, but the presence of the interdental projection in the left valve and the cutting away of the interdentum in the right valve opposite it, relates *Arkansia*, *Arcidens*, and *Lasmigona*.

This species was not found in the Tennessee River by Ortmann (1918, 1924, 1925), which strongly suggests that its present occurrence in Kentucky Lake behind an impoundment on the lower Tennessee River is the result of the recent introduction of fishes.

Range. Gulf Coastal Region: from the Colorado River system, Texas, east to the Tombigbee River drainage of the Mobile-Alabama-Coosa River system, Mississippi. Lower Mississippi River drainages. Ozarkian Region: Red, White and St. Francis river systems below the Ozark Crest; above it the Osage and Meramec river systems. Mississippian Region: Missouri River system; Illinois River; Mississippi River and drainages from Illinois north to Minnesota. Cumberlandian Region: lower Tennessee River, Tennessee. Ohioan Region: Wabash River drainage, Indiana; Green River drainage, Kentucky; Ohio River, east to Cincinnati, Hamilton Co., Ohio.

Reported from the St. Lawrence River System: Great Lakes Drainage (Lake Michigan) *Illinois*: Chicago, Cooke Co. by Baker (1906: 74) as in the State Laboratory, now the Illinois Natural History Survey, Urbana, Illinois. This record could not be verified there (Smith, pers. comm.) or at the Museum of Natural History of the University of Illinois, also at Urbana (Hoffmeister, pers. comm.). It is regarded as an erroneous record, since like other anodontine species *Arcidens* prefers the oozy mud of river margins where there is little current.

Abundance. "The species is rare but widely distributed" (Coker, 1919: 34).

Specimens Examined

Gulf Coastal Region

Colorado River System

Colorado River Drainage. *Texas:* Colorado River, Austin, Travis Co. (Strecker); Skull Creek, Colorado Co. (USNM).

Brazos River System

Brazos River Drainage: *Texas:* West Yegua Creek, Lee Co. (MZUM).

Buffalo Bayou System

Buffalo Bayou Drainage. *Texas:* Buffalo Bayou, near Eureka (MCZ), Houston (USNM); *both* Harris Co.

San Jacinto River System

San Jacinto River Drainage. *Texas:* San Jacinto River, Liberty Co. (MCZ, MZUM).

Trinity River System

Trinity River Drainage. *Texas:* Trinity River, Dallas (MCZ); Elm fork of Trinity River (Strecker); *both* Dallas Co. Trinity River (MZUM); Chambers Creek (Strecker); *both* Navarro Co.

Neches River System

Neches River Drainage. *Texas:* Neches River, Smith Co. (Strecker). Neches River, Big Eddy, Henderson Co. (Strecker). Poe Lake, Nacogdoches Co. (MZUM).

Sabine River System

Sabine River Drainage. *Texas:* Sabine River, Gladewater, Gregg Co. (Strecker). *Louisiana:* Sabine River, Logansport, De Soto Parish (MCZ).

Atchafalaya River System

Atchafalaya River Drainage. *Louisiana:* Bayou Waukasha, 3 mi. S of Lebeau, arm of Atchafalaya River, 10 mi. SE of Lebeau (*both* MCZ); *both* St. Landry Parish. Bayou Teche, St. Mary Parish (USNM).

Lake Maurepas-Pontchartrain-Borgne System

Louisiana: Baton Rouge, East Baton Rouge Parish (MCZ).

Pearl River System

Pearl River Drainage. *Mississippi:* Pearl River, Jackson, Hinds Co. (MCZ, USNM, MZUM).

Pascagoula River System

Chickasawhay River Drainage. [*Mississippi:* Chunkey Creek], Enterprise, [Clarke Co.] (Simpson, 1914: 476, as Enterprise, Alabama).

Mobile-Alabama-Coosa River System

Tombigbee River Drainage. *Mississippi:* Tombigbee River, Columbus, Lowndes Co. (MZUM).

Mobile River Drainage. *Alabama:* Mobile River, 30 mi. N Mobile, Mobile Co. (MCZ).

Lower Mississippi River Drainages

Tensas River System

Tensas River Drainge. *Louisiana:* branch of Tensas River, 15 mi. W Tallulah, Madison Co. (MZUM).

Big Black River System

Big Black River Drainage. *Mississippi:* Big Black River (Hinkley, 1906, Nautilus **20:** 53).

Yazoo River System

Yalabusha River Drainage. *Mississippi:* Yalabusha River, Grenada Co. (MZUM).

Ozarkian Region

Red River System

Red River Drainage. *Arkansas:* Mercer Bayou, N Black Diamond, Miller Co. (MCZ). *Louisiana:* Red River (MZUM) Caddo Lake, Chicot Bayou; Wallace Bayou; (*all* MZUM) *all* Caddo Parish. Frierson (USNM); Bayou Pierre (MZUM; CM); *both* De Soto Parish.

White River System

Black River Drainage. *Missouri:* Black River, Hendrickson, Butler Co. (MCZ).

Cache River Drainage. *Arkansas:* Cache River, Nemo, Craighead Co. (MZUM).

St. Francis River System

St. Francis River drainage. *Arkansas:* St. Francis River, Marked Tree, Poinsett Co. (MZUM).

Meramec River System

Meramec River Drainage. *Missouri:* Meramec River, Crawford Co. (Buchanan); Meramec River, Fern Glen, St. Louis Co. (MZUM).

Bourbeuse River Drainage. *Missouri:* Bourbeuse River, Franklin Co. (Buchanan).

Osage River System

Osage River Drainage. *Kansas:* Marais des Cygnes River, 3 mi. E Ottawa, Franklin Co. (Murray and Leonard). *Missouri:* Marais des Cygnes River, Rich Hill (MZUM), Papinsville (Utterback); *both* Bates Co.; Grand River, Henry Co. (MZUM); Grand River, Warsaw, Benton Co.; Osage River (*both* Utterback).

Mississippian Region

Missouri River System

James River Drainage. *South Dakota:* James River, near Frankfort, Spink Co.; James River, Riverside, Hanson Co. (*both* Coker and Southall).

Missouri River Drainage. *Missouri:* Lake Contrary, St. Joseph, Buchanan Co.; Platte River (*both* Utterback).

Mississippi River System

Big Muddy River Drainage. *Illinois:* Big Muddy River, DeSoto, Jackson Co.; Blairsville, Williamson Co.; Waltonville, Jefferson Co. (*all* Mus. Nat. Hist., Univ. Illinois, pers. comm.).

Kaskaskia River Drainage. *Illinois:* Kaskaskia River, Washington Co. (MCZ).

Mississippi River Drainage. *Illinois:* Mississippi River, Alton, Madison Co. (MCZ).

Illinois River Drainage. *Illinois:* Illinois River, 10 mi. below Hardin, Calhoun Co. (Bartsch; USNM). Illinois River, Meredosia, Morgan Co. (MCZ). Illinois River, Havana, Mason Co. (Parmalee). Illinois River, Peru (MCZ); Utica (Baker); *both* LaSalle Co.

Sangamon River Drainage. *Illinois:* Sangamon River, Springfield, Sangamon Co. (MCZ). Sangamon River, 4 mi. above Mahomet, Champaign Co. (Baker, 1922: 143).

Mississippi River Drainage. *Illinois:* Mississippi River, Quincy, Adams Co. (MCZ). Mississippi River, Warsaw, Hancock Co. (MCZ). *Iowa:* Mississippi River below Burlington, Des Moines Co. (MCZ). *Illinois:* Benton Slough, Henderson Co. (MCZ).

Rock River Drainage. *Illinois:* Pecatonica River (MCZ).

Mississippi River Drainage. *Illinois:* Mississippi River, Moline, Rock Island Co. (MCZ). *Iowa:* Mississippi River, Clinton, Clinton Co. (MCZ). *Wisconsin:* Mississippi River, Prairie du Chien, Crawford Co. (Baker). Mississippi River, Pierce Co. (Grier).

Minnesota River Drainage. *Minnesota:* Minnesota River, 2.8 mi. SW Bloomington, Hennepin Co. (Stansbery, OSM).

Cumberlandian Region

Tennessee River System

Tennessee River Drainage. *Tennessee:* Kentucky Lake (of Tennessee River) 6

mi. above New Johnsonville, Benton Co. (MCZ).

Ohioan Region

Ohio River System

Wabash River Drainage. *Indiana:* Wabash River, Posey Co. (MCZ). *Illinois:* Fox River, Richland Co.; Little Wabash River, Carmi, White Co.; (*both* MCZ).

Green River Drainage. *Kentucky:* Mud River, Rectors Bridge, 3 mi. E Dunmore, Muhlenberg Co.; Rough River, Dundee, Ohio Co.; (*both* MCZ). Pond River (MZUM).

Ohio River Drainage. *Ohio:* Ohio River, Cincinnati, Hamilton Co. (Sterki, 1907: 393).

Genus *Arkansia* Ortmann and Walker

Arkansia Ortmann and Walker 1912, Nautilus **25:** 97. Type species, *Arkansia wheeleri* Ortmann and Walker, original designation. This genus is monotypic.

Arkansia wheeleri Ortmann and Walker

Plate 11, figure 1
Distribution: Plate 8 A

Arkansia wheeleri Ortmann and Walker 1912, Nautilus **25:** 98, pl. 8 (Old River [a bayou of the Ouachita River], Arkadelphia, [Clark Co.], Arkansas; holotype MZUM 105514) Simpson, 1914, Cat. Naiades **1:** 478; Ortmann, 1921, Nautilus **34:** 141.

Description. Shell usually of medium size, reaching 80 mm in length, though occasionally exceeding 100 mm. Shell subrotund to subovate or subrhomboidal. Valves inflated, rather thick and solid. Anterior end regularly rounded. Posterior end somewhat truncate. Ventral margin regularly curved. Dorsal margin curved, forming a distinct angle with the obliquely descending posterior margin. Hinge ligament short. Anterior margin straight. Posterior ridge not prominent, usually rounded, but sometimes slightly biangulate. Umbos very prominent, projecting anteriorly and incurved over a large lunule, their sculpture consisting of two or three double-looped bars, the loops slightly swollen or tubercular; sculpture restricted to the extremity of the umbos. Posterior half of the disk sculptured with irregular, oblique folds, sometimes very faint, which curve upwards on the dorsal slope, and in front of the posterior ridge are crossed by numerous, irregular, radiating, small folds or wrinkles at right angles to the lines of growth; anterior portion of the disk smooth. Periostracum with a silky luster, dark reddish-brown or black, usually lighter toward the umbos, which in young shells are chestnut colored.

Left valve with two not strongly differentiated pseudocardinal teeth coalescing along the hinge line, the anterior one narrow and parallel with the hinge line, the posterior one somewhat wider and heavier, slightly separated from a strong projection of the interdentum, which is continuous with the lower lateral tooth and slopes gradually to its extremity; upper lateral low, the groove between deep, extending nearly to the umbo. Right valve with a single, strong pseudocardinal tooth, with a deep pit behind it to receive the anterior pseudocardinal tooth of the left valve, interdentum cut away to receive the interdental projection of the left valve; one short strong, lateral tooth. Muscle scars not much impressed. Nacre usually salmon colored above the pallial line, bluish-white, or entirely white below, rather thin, slightly iridescent with a wide, dark, prismatic border. Sexual differences not marked.

Length	Height	Width	
87	73	48	Old River, Arkadelphia, Clark Co., Arkansas. Paratype. Wheeler colln.
73.5	62	41	As above. Holotype MZUM.
35	33	23	As above. Paratype. Wheeler colln.

Anatomy and Breeding Season. The anatomy was discussed by Ortmann and Walker (1912, Nautilus **25:** 97–99) and on the basis of it, they recognized that this species belonged to the subfamily

Anodontinae. The species is bradytictic (Wheeler, 1918: 113).

Habitat. "Found in the shallow waters both on the sand bars and muddy bottoms, but like other anodontine species they prefer the oozy mud of the river margins where there is little or no current" (Wheeler, 1918: 113).

Remarks. Arkansia wheeleri Ortmann and Walker is not very closely related to any other species, except *Arcidens confragosus* (Say), a widely distributed species. In general, their external appearance is somewhat similar. In both the smaller series of radiating wrinkles and the curved folds on the dorsal slope are very much alike. Both have strong, oblique folds on the posterior half of the disk, but those of *Arkansia* more closely resemble those of *Amblema plicata* (Say). *Arkansia* has a heavier more inflated shell; the umbos are fuller, more projecting, and more anterior. The umbonal sculpture of *Arkansia* is comparatively simple and confined to the upper umbo, whereas that of *Arcidens* is developed into strong pitched up nodules, at the base of the loops, and extends out onto the disk. The lateral teeth are better developed in *Arkansia* than in *Arcidens*, but the presence of the interdental projection in the left valve and the cutting away of the interdentum in the right valve opposite it, relates *Arkansia*, *Arcidens* and *Lasmigona*.

The Wheeler collection is in the Alabama Museum of Natural History, University of Alabama, University, Alabama, but was not available for study.

Range. Found only in the Ozarkian Region: below the Ozark Crest in the upper Red and Black river systems.

Abundance. "Has apparently never been found in numbers. The only recent record is from the Kiamichi River in Oklahoma" (Stansbery, 1970: 18).

Specimens Examined

Red River System

Kiamichi River Drainage. *Oklahoma:* Kiamichi River, Antlers, Pushmataha Co. (CM); Kiamichi River, 8.5 mi. NE Hugo, Choctaw Co. (USNM).

Little River Drainage. *Arkansas:* Little River, White Cliffs, Little River Co. (MZUM).

Black River System

Ouachita River Drainage. *Arkansas:* Ouachita River and Old River, *both* Arkadelphia, Clark Co. (*both* MCZ and MZUM).

Tribe LAMPSILINI
Genus *Actinonaias* Crosse and Fischer

Actinonaias Crosse and Fischer 1893, Recherches Zoologiques ... de l'Amerique Centrale et du Mexique, Pt. 7, **2**: 600. Type species, *Unio sapotalensis* Lea, monotypic. Frierson, 1917, Nautilus **31**: 48. Ortmann, 1919, Mem. Carnegie Mus. **8**: 232.

Ortmanniana Frierson 1927, Check list N American naiades, pp. 11, 79. Type species, *Unio carinatus* Barnes, original designation.

Venustaconcha Frierson 1927, Check list N American naiades, pp. 11, 81, Errata et corrigenda. Type species, *Unio venustus* Lea, original designation.

Actinonaias rafinesqueana (Frierson)
Plate 11, figures 2–4
Distribution: Plate 8 B

Lampsilis rafinesqueana Frierson 1927, Check list N American naiades, p. 69 ([Illinois River], Moodys, [Cherokee Co.], Oklahoma; holotype MZUM 87576 figured by Frierson, 1928, Nautilus **41**: 138, pl. 1, figs. 1, 2).

Actinonaias streckeri Valentine and Stansbery 1972, Sterkiana no. 42, p. 32, non Frierson 1927.

Description. Shell medium to large, often exceeding 100 mm in length. Outline long, elliptical. Valves subinflated, subsolid, slightly inequilateral. Anterior end regularly rounded. Posterior end ending in a point or biangulation below the medial line. Ventral margin regularly curved. Dorsal margin straight, forming an angle with the obliquely descending posterior margin. Hinge ligament long. Posterior ridge generally indistinct and faintly double. Umbos rather full, not much projected above the hinge line, their sculpture not observed, located con-

siderably forward of the middle of the shell. Surface of the shell smooth, except for wide growth rests. Periostracum dirty yellowish-green, or tawny, often marked by faint, broad, broken, greenish rays.

Left valve with two triangular pseudocardinal teeth of about equal height, and two lateral teeth. Right valve with a strong tooth in front of the umbo, with a smaller one before it. Interdentum narrow and flat. One lateral tooth. Anterior and posterior muscle scars, and pallial line, all well impressed. Nacre bluish-white to creamy, with a wide prismatic border.

Male shells are long elliptical, somewhat biangulate, posteriorly. Female shells are more rounded and expanded posteriorly, having a slight, wide marsupial swelling. Both male and female shells gape slightly at the anterior base.

Length mm	Height mm	Width mm	
104	62	35	White River, Cotter, Baxter Co., Arkansas. Male.
86	60	35	[Illinois River], Moodys, Cherokee Co., Oklahoma. Holotype. Female.

Anatomy and Breeding Season. Gordon (pers. comm.) has studied the anatomy, and in a work in preparation, on the basis of the "mantle flaps" will show that this species belongs in the genus *Lampsilis*. If this is so, then arguing heuristically, so will *A. pectorosa*.

Remarks. Actinonaias rafinesqueana (Frierson) bears a very close resemblance to the Cumberlandian species, *A. pectorosa* (Conrad). Females, of the former species, are more fan shaped posteriorly, and while both species generally have a similar dirty yellowish green periostracum, most specimens of *rafinesqueana* are generally slightly rayed or rayless, whereas specimens of *pectorosa* are almost always rayed. In both species the rays, when present, are characteristically broken.

In the Ozarkian Region, *rafinesqueana* can be confused with *A. ligamentina* (Lamarck), but the latter has a much heavier shell, a stronger posterior ridge, is more heavily rayed, and usually has a more greenish or brownish periostracum. *A. rafinesqueana* has also been confused with *Lampsilis powelli* (Lea), but the latter shell is proportionally longer, brighter yellow, and is without rays.

Range. Found only in the Ozarkian Region, below the Ozark Crest, in the upper Arkansas and White river systems.

Abundance. Apparently never taken in large numbers.

Specimens Examined

Arkansas River System

Verdigris River Drainage. *Oklahoma:* Verdigris River (Gordon, pers. comm.).

Neosho River Drainage. *Missouri:* Spring River [Jasper Co.]; Elk River, [McDonald Co.] (*both* Nordstrom *et al.* 1977: 19); Indian Creek [of Elk River]; McDonald Co. (figured allotype, MZUM [lost]).

Illinois River Drainage. *Oklahoma:* [Illinois River], Moodys, Cherokee Co. (Holotype MZUM 87576; paratypes MZUM 90665; paratype ANSP 145238).

White River System

White River Drainage. *Arkansas:* White River, Monte Ne, Benton Co.; White River, Cotter, Baxter Co. (*both* MCZ).

Black River Drainage. *Arkansas:* Black River (MZUM).

Genus *Lampsilis* Rafinesque

Lampsilis Rafinesque 1820, Ann. Gén. des Sci. Physiques (Bruxelles) **5**: 298. Type species, *Unio ovatus* Say, subsequent designation. Herrmannsen, 1847, Indicis Generum Malacozoorum **1**: 575. Frierson (1927: 11, 79) introduced under *Lampsilis*, the subgenus *Ortmanniana*. Type species, *Unio carinatus* Barnes, original designation. He included *L. abrupta* and *higginsi* in this subgenus. Ortmann (1919: 233) had already placed *carinatus* [=*ligamentina* (Lamarck)] under *Actinonaias* Crosse and Fisher 1893 because its anatomy was not that of a *Lampsilis*.

Lampsilis abrupta (Say)
Plate 12, figures 1, 2
Distribution: Plate 2

Unio abruptus Say 1831, American Conch. no. 2 [letter press], pl. 17 (Wabash [River, New Harmony, Posey Co., Indiana], type ANSP [lost], *teste* Johnson and Baker, 1973, Proc. Acad. Nat. Sci. Phila. **125:** 146).

Unio cyclips Rafinesque 1831. Cont. Monog. Bivalve Shells River Ohio, p. 2 (river[s] Ohio and Mississippi, type ANSP [lost], *teste* Johnson and Baker, 1973, Proc. Acad. Nat. Sci. Phila. **125:** 146).

Unio orbiculatus Lea 1836, Synopsis Naiades, p. 25, *non* Hildreth 1827.

Unio crassus Conrad 1836, Monography Unionidae, no. 2, p. 34, pl. 16 (rivers of Ohio, Indiana and Illinois, type ANSP [lost], *teste* Johnson and Baker, 1973, Proc. Acad. Nat. Sci. Phila. **125:** 145) *non* Say 1817.

Lampsilis orbiculata Simpson 1914, Cat. Naiades **1:** 76. Coker, 1919, Bull. U. S. Bur. Fisheries for 1917–18, **36:** 29, pl. 14, lower fig. Ortmann, 1919, Mem. Carnegie Mus. **8:** 320 [description *partim*], pl. 20, fig. 8, pl. 21, figs. 1, 2. Neel and Allen, 1964, Malacologia **1:** 448, fig. 53. Parmalee, 1967, Illinois State Mus. Pop. Sci. Ser. **8:** 67, pl. 23 B. La Rocque, 1967, Ohio Geol. Surv. Bull. no. 62 (2): 217, fig. 103, fig. 104 distributional map [*partim*]. *All non* Hildreth 1827.

Lampsilis (*Ortmanniana*) *abrupta* (Say). Frierson, 1927, Check list N American naiades, p. 80. Haas, 1969, Das Tierreich, pt. 88, p. 461.

Lampsilis orbiculata forma *orbiculata*. Starrett, 1971, Illinois Nat. Hist. Surv. Bull. **30** (5): 338.

Description. Shell medium to large, sometimes exceeding 100 mm in length. Outline subelliptical, subovate or subquadrate; gaping at the anterior base. Valves somewhat inflated; extremely thick and heavy. Anterior end regularly rounded; posterior end pointed in males, abruptly truncated in females. Ventral margin regularly rounded in males, almost straight in females. Dorsal margin short and slightly curved, forming an indistinct angle with the obliquely descending posterior margin. Hinge ligament long and full. Posterior ridge visible in males and younger specimens, indistinct in older females. Posterior slope slightly convex or flattened, narrow. Umbos moderately inflated, projecting a little above the hinge line, their sculpture not distinct, more or less inclined forward, located in front of the middle of the shell. Surface of the shell smooth, except for wide, low, concentric ridges. The rest periods are often marked by a sulcus. Periostracum subshiny or dull, light or dark, yellow, yellowish brown. Rays, seldom present, except in younger shells; when visible they are grayish green or brownish and are usually fine and widely spaced.

Left valve with two triangular pseudocardinal teeth of about equal height, two curved lateral ones. Right valve with one high triangular pseudocardinal, with a smaller low one before and behind it. Interdentum narrow and flat. One strong lateral tooth. Anterior and posterior adductor muscle scars, and pallial line, all well impressed. Nacre generally silvery-white, iridescent, sometimes salmon tinted.

Male shells are subelliptical or subovate, the regularly curved ventral and posterior margins meeting in a blunt point mid-way from the base. Female shells develop a post-basal swelling which renders them posteriorly subtruncate or subquadrate in outline.

Length mm	Height mm	Width mm	
103	75	61	Ohio River, Portsmouth, Scioto Co., Ohio. Male. (CM).
93	65	43	Ohio River. Male.
92	83	57	Ohio River, Industry, Beaver Co., Pennsylvania. Female. (CM).
73	68	42	Ohio River. Female.

Anatomy and Breeding Season. The anatomy was discussed by Ortmann (1912: 353) and Simpson (1914: 76). The glochidia were figured by Ortmann (1911, pl. 89, fig. 22) 0.19 × 0.21 and 0.20 × 0.25 mm. This species is bradytictic (Ortmann, 1919: 323).

Habitat. Found on riffles in the strong currents of large rivers (Ortmann, 1919: 324).

Remarks. Lampsilis abrupta (Say) in

the Cumberlandian and Ohioan regions is easily recognized, except for young shells, by the thickness of the shell, which for its size is probably the heaviest shell in those regions. Also characteristic is its yellowish brown periostracum which may have narrow, widely spaced green rays. Young males resemble those of *Actinonaias ligamentina* (Lamarck) but the latter usually have wide green rays which are close together. The female of *L. abrupta* does not resemble *A. ligamentina*. In the Mississippian and the Ohioan regions *L. abrupta* may be mistaken for *L. higginsi* (Lea), see: Remarks.

Frierson (1924: 135) showed that Lea (1836: 25) had mischievously misidentified *Unio orbiculatus* Hildreth 1827 as *Unio abruptus* Say 1831. Hildreth's type measured 100 mm in length, 100 mm in height, and had a purple [or] violet nacre. These data clearly indicate that *orbiculatus* is not *abruptus* Say which is never as long as wide, and does not have a purple nacre. In a sample of 74 specimens of *L. abrupta*, Ball (1922: 113) was unable to reconcile Hildreth's measurements with those of his specimens. *Unio orbiculatus* Hildreth is *Obovaria retusa* (Lamarck 1819).

Range. Cumberlandian Region: Tennessee and Cumberland river systems. Ohioan Region: Monongahela and Allegheny rivers above maximum glaciation; Ohio River proper; and the Wabash, Scioto, and Muskingum rivers; St. Lawrence River System, western Lake Erie. Mississippian Region: Illinois River drainage, Illinois.

Abundance. Apparently never taken in large quantities. Ortmann (1919: 323) found it most abundant in the Ohio River, Beaver Co., Pennsylvania, and said that he had not collected more than two dozen specimens below Pennsylvania. Stansbery (1970: 19) said that "This species is still taken occasionally in the Tennessee River below Wilson and Guntersville Dams, and rarely in the Muskingum River, Ohio."

Specimens Examined

Mississippian Region

Mississippi River System

Illinois River Drainage. *Illinois:* Illinois River, 1 mi. below Hardin, Calhoun Co. (Bartsch, USNM); Illinois River, Peoria Lake, Chillicothe, (*both* Danglade), *both* Peoria Co.; Illinois River, La Salle, La Salle Co. (MZUM).

Ohioan Region

Ohio River System

Ohio River Drainage. *Illinois:* Ohio River, Brookport, Massac Co. (Parmelee). *Kentucky:* Ohio River, Paducah, McCracken Co. (Bartsch, USNM).

Cumberlandian Region

Tennessee River System

Clinch River Drainage. *Tennessee:* Clinch River, Offutt (CM); Clinch River, .5 mi. below dam at Norris (MZUM); *both* Anderson Co.; Clinch River, Solway, Knox Co. (CM).

Holston River Drainage. *Tennessee:* Holston River (MZUM).

French Broad River Drainage. *Tennessee:* French Broad River (MCZ).

Tennessee River Drainage. *Tennessee:* Tennessee River, Washington Ferry, Meigs Co. (MZUM).

Flint River Drainage. *Tennessee:* Flint River (MZUM).

Tennessee River Drainage. *Alabama:* Tennessee River, 11 mi. S Huntsville, Madison Co. (MZUM).

Limestone Creek Drainage. *Alabama:* Limestone Creek, The Points, Mooresville, Limestone Co. (MZUM).

Tennessee River Drainage. *Alabama:* Tennessee River, Decatur, Morgan Co. (MZUM); Tennessee River, Muscle Shoals (MZUM), Florence (MCZ, MZUM), *both* Lauderdale Co.; Tennessee River, Tuscumbia, Colbert Co. (MCZ).

Duck River Drainage: *Tennessee:* Duck River, Columbia, Maury Co. (MZUM).

Tennessee River Drainage. *Tennessee:* Tennessee River, Trotter's Landing, Humphreys Co. (MZUM). Tennessee River, 1 mi. above Fort Henry, Steward Co. (MZUM).

Cumberland River System

Cumberland River Drainage. *Kentucky:* Cumberland River, Robertsport; Monticello; (*both* MZUM) *both* Wayne Co. Cumberland River, below Wolf Creek Dam; Horse Shoe Bottom Ferry; below Rowena; (*all* MZUM) *all* Russell Co. Cumberland River, Burkesville; Neely's Ferry, 4 mi. S Burkesville; (*both* MZUM) *both* Cumberland Co.

Obey River Drainage. *Tennessee:* Obey River, mouth of Jolly Creek, Picket Co. (MZUM). Obey River, mouth of Horse Creek, Clay Co. (MZUM).

Cumberland River Drainage. *Tennessee:* Cumberland River, Hartsville, Trousdale Co. (Manning coll'n.). Nashville, Davidson Co. (MCZ). Cumberland River, Gowers Island [between Nashville and Dover] (MZUM).

Ohioan Region

Ohio River System

Wabash River Drainage. *Indiana:* Wabash River, Lafayette, Tippecanoe Co. (MZUM). White River (Call, 1898: 493).

Ohio River Drainage. *Indiana:* Ohio River, Vevay, Switzerland Co. (MZUM). *Ohio:* Ohio River, Constance, Boone Co. (MCZ). Ohio River, Cincinnati, Hamilton Co. (MCZ; MZUM). Ohio River, below New Richmond, Clermont Co. (MZUM).

Scioto River Drainage. *Ohio:* Scioto River, Chillicothe, Ross Co. (MZUM).

Ohio River Drainage. *Ohio:* Ohio River, Portsmouth, Scioto Co. (CM). Ohio River, Portland, Meigs Co. (CM). *West Virginia:* Ohio River, Parkersburg, Wood Co. (CM). *Ohio:* Ohio River, Marietta, Washington Co. (MCZ).

Muskingum River Drainage. *Ohio:* Muskingum River (Stansbery, 1970: 19).

Ohio River Drainage. *West Virginia:* Ohio River, St. Marys, Pleasants Co. (CM). *Ohio:* Ohio River, Toronto (CM); Shanghae [Knox Township] (MCZ); *both* Jefferson Co. *Pennsylvania:* Ohio River, Industry, Cooks Ferry, Shippingport; (*all* CM) *all* Beaver Co.

Allegheny River Drainage. *Pennsylvania:* Allegheny River, Kelly, Godfrey; (*both* CM) *both* Armstrong Co.

Monongahela River Drainage. *Pennsylvania:* Monongahela River, Charleroi, Washington Co. (CM).

St. Lawrence River System

Great Lakes Drainage (Lake Erie): Niagara River, Buffalo, [Erie Co.]. The single specimen collected by Miss Walker in 1906, reported by Robertson and Blakeslee (1948: 111), as in the Buffalo Museum of Science, could not be located (H. W. Charnley, pers. comm.). Since Robertson and Blakeslee describe *A. ligamentina*, and the above specimen separately, the record is accepted as authentic.

Lampsilis higginsi (Lea)

Plate 13, figures 1, 2
Distribution: Plate 2

Unio higginsii Lea 1857, Proc. Acad. Nat. Sci. Phila. **9:** 84 ([Mississippi River], Muscatine, [Muscatine Co.], Iowa); 1862, Jour. Acad. Nat. Sci. Phila. (2) **5:** 188, pl. 24, fig. 258, figured holotype USNM 84823; 1863, Obs. Unio **9:** 10.

Lampsilis higginsii grandis Simpson 1914, Cat. Naiades **1:** 78 (Illinois River, near Utica, [Lasalle Co.], Illinois, type USNM [lost]).

Lampsilis higginsii (Lea). Simpson 1914, Cat. Naiades **1:** 78. Utterback, 1916, Amer. Midl. Nat. **4:** 445 [182], pl. 28, figs. 105 A and B. Coker, 1919, Bull. U. S. Bur. Fisheries for 1917–18, **36:** 29, pl. 14, middle pair. Baker, 1928, Wisconsin Geol. and Nat. Hist. Surv., Bull. **70:** (2): 293, pl. 95, Parmalee, 1967, Illinois State Mus. Pop. Sci. Ser. **8:** 67, pl. 23: A.

Lampsilis (*Ortmanniana*) *higginsii* (Lea). Frierson, 1927, Check list N American naiades, p. 80. Haas, 1969, Das Tierreich, pt. 88, p. 461.

Lampsilis orbiculata forma *higginsii* (Lea). Starrett, 1971, Illinois Nat. Hist. Surv. Bull. **30** (5): 339.

Description. Shell medium to large, sometimes exceeding 100 mm in length. Outline elliptical, oval, or rhomboid, gaping at the anterior base. Valves much inflated, thick and heavy. Anterior end regularly rounded; posterior end somewhat pointed in males; truncated or subtruncated in females. Ventral and dorsal margins slightly curved, the latter forming an indistinct angle with the obliquely descending posterior margin. Hinge ligament long and full. Posterior ridge rather sharp in some males and younger specimens, indistinct in older females. Posterior slope slightly convex or flattened, narrow. Umbos swollen, inflated, considerably raised above the hinge line, their sculpture consisting of a few, slightly looped, feeble ridges, located considerably forward of the middle of the shell. Surface of the shell smooth, except for wide, low, concentric ridges. The rest periods are often marked by a sulcus. Periostracum usually dull and dark, yellowish to olive. Rays frequently present, green and often wide.

Left valve with two triangular pseudocardinal teeth of about equal height, two curved lateral ones. Right valve with one high triangular pseudocardinal, with a smaller low one before and behind it. Interdentum narrow and flat. One strong lateral tooth. Anterior and posterior adductor muscle scars, and pallial line, all well impressed. Nacre generally silvery-white, iridescent, sometimes salmon tinted, yellowish or orange.

Male shells are elliptical or oval, the regularly curved, ventral dorsal margins meeting, often imperceptibly, mid-way from the base. Female shells develop a post-basal swelling which renders them posteriorly subtruncate and rhomboidal in outline. They also become greatly inflated.

Length mm	Height mm	Width mm	
97	68	56	Mississippi River, Mercer Co., Illinois. Male.
88	63	45	Illinois River, Illinois. Male.
100	76	69	Illinois River, Meredosia, Morgan Co., Illinois. Female.
91	69	63	Mississippi River, Davenport, Scott Co., Iowa. Female (MZUM).
96	72	59	Spring River, Lawrence Co., Arkansas. Male. (MZUM).
78	62	45	Old River, Arkadelphia, Clark Co., Arkansas. Female (MZUM).

Anatomy and Breeding Season. The anatomy of *higginsi* and *abrupta* have not been separately discussed. A glochidium of the former was figured by Surber (1912: 9, pl. 2, fig. 23) which measured 0.21 × 0.26 mm. He also (1912: 7) indicated that this species is bradytictic, and (1913: 107) that *Stizostedion canadense* (Smith) is [at least one of] its natural host fish.

Habitat. Found on riffles in the strong currents of large rivers.

Remarks. In the Mississippian region *Lampsilis higginsi* can be confused with *Obovaria olivaria* (Rafinesque), but the latter has a more regularly ovate shell, fine, rather than broad green rays, and more especially it has only a slight interdentum between the most posterior pseudocardinal tooth and the lateral teeth in the right valve and none in the left valve. *L. abrupta* and *higginsi* overlap in their distribution in the Illinois and lower Ohio rivers.

Simpson (1914: 76, 78) correctly described *L. abrupta* and *higginsi*. Ortmann (1919: 320) included both in his description, and suggested there was only one species, as did H. and A. van der Schalie (1950: 456). An examination of the specimens available to them revealed misidentifications which led to their erroneous conclusion. Morrison in writing to Starrett (1971: 338) noted that, "The geographic range of *abruptus* overlaps that of *higginsi* in the region of the Ohio-Mississippi confluence," and that they were distinct species. Starrett (1971: 338), however, followed the classification

suggested by Stansbery which implies they are a single species, since "forms" have no status in modern nomenclature. Stansbery and Kokai (1979: 57) later suggested, "that there are several distinct taxa within this [*Lampsilis orbiculata*] complex," without any further elucidation.

L. higginsi differs from *abrupta* in that the former has umbos which are much higher and fuller. The shells of both sexes in *L. higginsi* are more inflated, the females often being very bulbous, while those of *abruptus* are rather flat sided. *L. higginsi* has a darker greenish periostracum in contrast to the yellowish periostracum of *abrupta*. The rays of *L. higginsi* are broader and green rather than grayish green or brownish as in *abrupta*.

Range. Ozarkian Region: below the Ozark Crest in the Black and White river systems; and above it in the Meramec and Gasconade river systems. Mississippian Region: Illinois River; Mississippi River from Illinois north to Wisconsin. Ohioan Region: lower Ohio River, Illinois. Listed by Gordon, *et al.* (1980: 35) as occurring in the Little River Drainage of the Red River System, Arkansas. These specimens, in the MZUM, were examined by the author and are *Lampsilis satur* (Lea), a species not included in their list.

Abundance. "Is a rather uncommon species, but a few may be found in almost any carload of mixed shells" (Coker 1919: 29). "Is known living today only in the upper Mississippi River" (Stansbery 1970: 19). Listed as a rare and endangered species by Stansbery (1971: 15). In the area between Pairie du Chien, Crawford Co., Wisconsin and Harpers Ferry, Alamakee Co., Iowa, Mathiak (1979: 57, pl. 3, 10 C) collected 40 live specimens in five days during 1975. He said that, "in any calculation taking into account the number of tons of shells being processed [by fisheries] daily, the number of Higgin's Eye mussels I found in a few hours would lead to the conclusion that hundreds had actually been harvested in 1975." He further noted, "no one working with the endangered species program took the opportunity to search for the Higgin's Eye or other rare mussels during [1974–1975] when all the species were being harvested from the Prairie du Chien area." The collecting by Fuller (1978: 3) offers further evidence that *L. higginsi* is probably about as abundant in the upper Mississippi River as it was early in the century. It would appear that this species was placed on the endangered list by over enthusiastic bureaucrats. This would be of little importance if it did not lead directly to the unnecessary harassment of commercial fishermen.

Specimens Examined

Ozarkian Region

Black River System

Ouachita River Drainage. *Arkansas:* Ouachita River (MZUM), Old River (MZUM, CM), *both* Arkadelphia, Clark Co.

Saline River Drainage. *Arkansas:* Sabine [sic] = Saline River (Stansbery, 1970: 19).

White River System

White River Drainage. *Arkansas:* North Fork White River, nr. Norfork, Baxter Co. (MCZ).

Black River Drainage. *Arkansas:* Black River, above Pocahontas, Randolph Co. (MZUM, CM): Black River, Black Rock, Lawrence Co. (MCZ, MZUM, USNM).

Spring River Drainage. Spring River [Lawrence Co.] (MZUM).

Meramec River System

Meramec River Drainage. *Missouri:* Meramec River, Crawford, Franklin, and St. Louis Cos. (Buchanan).

Gasconade River System

Gasconade River Drainage. *Missouri:* Gasconade River (Stansbery, 1970: 19).

Mississippian Region

Missouri River System

Missouri River Drainage. *Nebraska:* Nemeha River (Aughey, 1877: 702).

Mississippi River System

Illinois River Drainage. *Illinois:* Illinois River, 1 mi. below Hardin (Bartsch, USNM; MZUM); Kampsville (Danglade); *both* Calhoun Co. Illinois River, Florence, Pike Co. (Danglade). Illinois River, Meredosia, Morgan Co. (MCZ). Illinois River, Beardstown, Cass Co. (Danglade). Illinois River, Bath (Danglade); Havana (MZUM); *both* Mason Co. Illinois River, Peoria (Danglade; Parmalee); Chillicothe (Danglade); *both* Peoria Co. Illinois River, Marquette, Bureau Co. (Shimek, USNM). Illinois River, nr. Utica, La Salle Co. (Simpson). Illinois River, Morris, Grundy Co. (Shimek; USNM). Kankakee River (MZUM).

Mississippi River Drainage. *Missouri:* Mississippi River, Louisiana, Pike Co. (Utterback). Mississippi River, Hannibal, Marion Co. (Utterback). *Iowa:* Mississippi River, Montrose, Lee Co. (Bartsch, USNM). Iowa River, Iowa City, Johnson Co. (Shimek, USNM). Mississippi River, Muscatine (USNM); Fairport (Morrison, USNM); Montpelier (Bartsch, USNM); *all* Muscatine Co. Mississippi River, Buffalo (MZUM); Davenport (MCZ); Princeton (Bartsch, USNM); *all* Scott Co., Crooked Slough, 1 mi. N Bellevue, Jackson Co. (Bartsch, USNM). Mississippi River, Dubuque, Dubuque Co. (Sharpe, USNM). *Wisconsin:* Wisconsin River, Arena, Iowa Co. (MCZ). Mississippi River, Prairie du Chien (Stansbery, Ohio State Museum 38489, 21 fresh specimens, 1976); Lynxville (Bartsch USNM); *both* Crawford Co. Mississippi River, Victory; Genoa; Stoddard; (*all* Bartsch, USNM); *all* Vernon Co. Black River, between R. R. bridge and La Crosse, La Crosse Co. (Bartsch, USNM). *Minnesota:* Mississippi River Dresback, Winona Co. (Bartsch, USNM). *Wisconsin:* Mississippi River, Buffalo, Buffalo Co. (Grier). *Minnesota:* Lake Pepin, Red Wing, Goodhue Co. (MCZ; USNM). *Wisconsin:* Mississippi River, above Prescott, Pierce Co. (Bartsch, USNM). St. Croix River, Hudson, St. Croix Co. (MZUM).

Ohioan Region

Ohio River System

Ohio River Drainage. *Illinois:* Ohio River, Hillerman, Massac Co. (Bartsch, USNM).

Lampsilis powelli (Lea)

Plate 15, figures 3, 4

Distribution: Plate 8 B

Unio powellii Lea 1852, Trans. Amer. Philos. Soc. **10:** 270, pl. 19, fig. 25 (Saline River, Arkansas; figured holotype USNM 85042); 1852, Obs. Unio **5:** 26.

Lampsilis powellii (Lea). Simpson, 1914, Cat. Naiades **1:** 75. Scammon, 1906, Kansas Univ. Sci. Bull. **3:** 288. Utterback, 1916, Amer. Midl. Nat. **4:** 446 [183], pl. 28, fig. 103 A, B [figured as *L. luteola*], Black River, Williamsville, Wayne Co., Missouri, MCZ 271445. Isely, 1925, Proc. Oklahoma Acad. Sci. **4:** 111.

Description. Shell generally of medium size, occasionally large, exceeding 100 mm in length. Outline elliptical or long obovate. Valves subinflated, rather thin to subsolid. Anterior end regularly rounded. Posterior end somewhat pointed. Ventral margin regularly curved, or straight. Dorsal margin straight forming a barely perceptable angle with the obliquely descending posterior margin. Hinge ligament long. Posterior ridge indistinct. Umbos moderately full, slightly projected above the hinge line, their sculpture consisting of double looped corrugations, located considerably forward of the middle of the shell. Surface of the shell smooth except for growth rests. Periostracum generally shining, olive-brown, tawny, and always without rays.

Left valve with two triangular pseudocardinal teeth (the anterior one higher), and with two lateral teeth. Right valve

with one strong pseudocardinal tooth in front of the umbo and with a smaller one before it. Interdentum very narrow. One lateral tooth. Anterior adductor muscle scars well impressed, posterior ones less so. Pallial line visible anteriorly. Nacre bluish white and iridescent.

Male shells are feebly biangulate posteriorly, near the medial line. Female shells are wider and rounder posteriorly.

Length mm	Height mm	Width mm	
80	56	29	Saline River, Arkansas. Holotype. Male.
77	39	24	As above. Allotype. Female.

Anatomy and Breeding Season. Unknown.

Remarks. Lampsilis powelli (Lea) bears a very close resemblance to the Cumberlandian species, *L. virescens* (Lea) which is found only in the Tennessee River system, mainly in the Paint Rock River drainage. Shells of the former are always without rays, while those of *virescens* usually have green rays above the sometimes marked posterior ridge. In the Ozarkian Region, *powelli* has been confused with *L. radiata siliquoidea, hydiana, teres,* and *Villosa reeviana.* With the exception of *L. teres,* which is sometimes without rays, all of these other species are rayed to some degree. *L. powelli* differs from *teres,* in that the latter is more elongate, and pointed, much more inflated, and the females exhibit more sexual dimorphism.

Range. Found only in the Ozarkian Region, below the Ozark Crest, in the Saline River drainage of the Black River system; the upper Arkansas, and upper White River systems.

Abundance. Apparently never taken in large numbers.

Specimens Examined

Black River System

Saline River Drainage. *Arkansas:* Saline River, Benton, Saline Co. (MCZ, MZUM).

Arkansas River System

Neosho River Drainage. *Kansas:* Neosho River, Oswego (Scammon, 1906: 288); Chetopa (Isely, 1925, Table 2); *both* Labette Co. Spring River, Baxter Springs, Cherokee Co. (MCZ). *Missouri:* Elk River, McDonald Co. (Utterback, 1916: 183).

Illinois River Drainage. *Oklahoma:* Illinois River, Moodys, Cherokee Co. (Isely, 1925: 67).

White River System

White River Drainage. *Missouri:* White River (Utterback, 1917, Table).

Black River Drainage. *Missouri:* Black River, Williamsville, Wayne Co. (MCZ).

Genus *Proptera* Rafinesque

Potamilis Rafinesque 1818, Amer. Monthly Mag. and Critical Rev. [New York] **3:** 355. Type species, *Unio alatus* Say, monotypic. In 1818, 23 of the 24 taxa listed under *Potamilis* were *nomina nuda.* Morrison (1969: 24) correctly stated that no. 12, *P. alatus* is *Unio alatus* Say 1817. Say had sent Rafinesque a copy of his article from the first edition of *Nicholson's Encyclopedia* (Johnson, 1975: 265).

Proptera Rafinesque 1819, Jour. Phys. Chim. Hist. Nat. [Paris] **88:** 426. Type species, *Unio alatus* Say. Subsequent designation, Herrmannsen, 1847, Indicis Generum Malacozoorum **2:** 41, under *Metaptera* Rafinesque, an objective synonym of *Proptera. Metaptera* Rafinesque 1820, Ann. Gén. Sci. Physiques, Bruxelles **5:** 299. Rafinesque deemed *Proptera* inappropriate. *Potamilis* was overlooked from 1818 until its availability was indicated by Morrison (1969: 24). It was adopted by Valentine and Stansbery (1971: 25), and has since been promulgated by the latter. *Proptera* has been in general usage since 1900 (Simpson, 566). As no question of priority of authorship is involved, the resurrection of *Potamilis* appears nugatory. The most recent revision of the *Rules* (1974, Bull. Zool. Nomencl. **31** (2): 80) under Article 23, states: "A zoologist who considers that the application of the Law of Priority would in his judgment disturb stability or universality or cause confusion is to maintain the existing usage and must refer the case to the Commission for a decision under the plenary powers [Art. 79]." This author maintains existing usage, and suggests that those who would promulgate *Potamilus* seek the ruling.

Proptera capax (Green)

Plate 16, figures 1, 2

Distribution: Plate 3

Unio capax Green 1832, Cabinet of Nat. Hist. and Amer. Rural Sports **2:** 290 ([Mississippi River],

Falls of St. Anthony [Minneapolis, Hennepin Co., Minnesota], type [lost]; Bayou Teche [error]).

Symphynota globosa Lea 1832, Trans. Amer. Philos. Soc. **5:** 41, pl. 4, fig. 12 (River Ohio, 150 miles below Louisville [Kentucky], figured type [lost]; syntypes ANSP 56609); 1834, Obs. Unio **1:** 153. Lea (1852, Synopsis of Naiades, third edit., p. 27) acknowledged that *capax* had priority over *globosa*.

Lampsilis capax (Green). Smith, 1899, Bull. U. S. Bur. Fisheries for 1898, pl. 84. Simpson 1914, Cat. Naiades **1:** 76; Coker, 1919, Bull. U. S. Bur. Fisheries for 1917–18, **36:** 31, pl. 17, lower fig.

Proptera capax (Green). Ortmann, 1914, Nautilus **28:** 67. Utterback, 1916, Amer. Midl. Nat. **4:** 394 [162], pl. 26, figs. 93 A and B. Frierson, 1927, Check list N American naiades, p. 87. Baker, 1928, Wisconsin Geol. and Nat. Hist. Sur., Bull. **70** (2): 248, pl. 84, figs. 1–4. Parmalee, 1967, Illinois State Mus. Pop. Sci. Ser. **8:** 83, pl. 28: B. La Rocque, 1967, Ohio Geol. Surv. Bull. no. 62 (2): 260, fig. 149, fig. 150 distributional map. Starrett, 1971, Illinois Nat. Hist. Surv. Bull. **30** (5): 330.

Description. "The valves of this shell are much more convex or globose than any of the uniones which I have seen, and as they are quite thin compared with most of the western species, the cavity in which the animal is lodged is exceedingly capacious—hence its name. The anterior end is broad, rounded, and slightly angular near the hinge; the posterior margin is very narrow, and also rounded; these valves do not close perfectly on each other, but gape at the opposite margins; this is more remarkable in old than in young individuals. The epidermis is smooth, yellowish, and frequently clouded with brown. The nacre is bluish white, and often very beautifully iridescent. The beaks are recurved over the tegument. The teeth resemble very much those of the *U. ovatus* of Mr. Say, but they are much thinner. These characters, I think, will be sufficient to distinguish the *Unio capax* from every other shell." The original description is quoted since it is quite unavailable, and because it is lucid.

Length mm	Height mm	Width mm	
128	90	74	Wabash River, New Harmony. Posey Co., Indiana.
92	77	61	As above.

Anatomy and Breeding Season. The anatomy was discussed by Ortmann (1914, Nautilus **24:** 67). The "axe-head" glochidium was figured by Coker and Surber (1911: 179, pl. 1, fig. 4, 4a). Reported gravid in June, July, August, and October (Surber, 1912: 7 and Ortmann, *loc. cit.*). Duration of the season not indicated.

Habitat. "Has been taken on both a sand and mud bottom, in flowing water, and at depths of only a few inches to eight feet or more" (Parmalee, 1967:83).

Remarks. Proptera capax (Green) may be easily recognized by its thin, globose shell with inflated umbos, and by its periostracum which is always rayless. It may be confused with *Lampsilis ovata* (Say) but the latter has a heavy shell, is not as globose, is generally rayed, and exhibits sexual dimorphism, which *capax* does not.

Coker and Surber (1911: 20) indicated that *capax* was not a *Lampsilis*, but a *Proptera*, where it was placed by Ortmann (1914, Nautilus **24:** 67).

Range. Found in the Ozarkian Region, only below the Ozark Crest, in the White and St. Francis river systems. Mississippian Region: Illinois River; Mississippi River from Illinois north to Minnesota. Ohioan Region; Wabash River; St. Lawrence River system, western Lake Erie and eastern Lake Ontario drainages.

Reported from the Arkansas River system, Neosho River, Lyon Co., Kansas, by Murray (1962, Nautilus **75:** 95). The single specimen found was figured by Murray and Leonard (1962: 132, pl. 36) and is a female of *Proptera purpurata* (Lamarck), with a heavy shell and characteristic purple nacre. The single male shell [no longer available] reported from the Verdigris River, Nowata Co., Oklahoma, by Branson (1963: 510), as *capax*, was probably also *P. purpurata*. *P. capax* does not exhibit sexual dimorphism.

Abundance. "Most numerous in the lower Ohio and Wabash rivers—especially in the latter" (Parmalee, 1967: 83). "Largely, if not entirely, gone from the

entire Ohio River drainage. This species still survives in the White and St. Francis rivers of Arkansas" (Stansbery, 1970: 18).

Specimens Examined

Ozarkian Region

White River System

White River Drainage. *Arkansas:* White River, 1 mi. NE Devall Bluff, Prairie Co. (MZUM).

St. Francis River System

St. Francis River Drainage. *Arkansas:* St. Francis River, Parkin (MCZ; MZUM); Wittsburg (Call); *both* Cross Co. St. Francis River, Madison, St. Francis Co. (MCZ; CM).

Mississippian Region

Missouri River System

Missouri River Drainage. *Nebraska:* Blue River; Elkhorn River (*both* Aughey, 1877: 702).

Mississippi River System

Mississippi River Drainage. *Illinois:* Mississippi River, Alton, Madison Co. (MCZ; MZUM).

Illinois River Drainage. *Illinois:* Illinois River, Grafton, Jersey Co. (Danglade). Illinois River, Kampsville, Calhoun Co. (Danglade). Illinois River, Pearl; Florence (*both* Danglade); *both* Pike Co. Illinois River, Beardstown, Cass Co. (Danglade). Sangamon River (Danglade). Illinois River, Havana, Mason Co. (Danglade). Spoon River, Fulton Co. (MZUM). Illinois River, Pekin, Tazewell Co. (Danglade). Illinois River, La Salle Co. (Calkins).

Mississippi River Drainage. *Illinois:* Mississippi River, Hamburg, Calhoun Co. (MCZ). *Missouri:* Mississippi River, Hannibal, Marion Co. (MCZ). Mississippi River, La Grange, Lewis Co. (Utterback). *Illinois:* Mississippi River, Hamilton (MZUM), Warsaw (MCZ); *both* Hancock Co. *Iowa:* Des Moines River, Keokuk, Lee Co. (MZUM). Mississippi River, Burlington, Des Moines Co. (MCZ). *Illinois:* Mississippi River, Mercer Co. (MCZ). *Illinois:* Mississippi River, Martins Landing, Rock Island Co. (MZUM). *Iowa:* Mississippi River, McGregor, Clayton Co. (MZUM). *Wisconsin:* Mississippi River, Alma, Buffalo Co. (MZUM). *Minnesota:* Mississippi River, Falls of St. Anthony, [Minneapolis, Hennepin Co.] (Green).

Ohio River System

Ohio River Drainage. *Illinois:* Ohio River, Hillerman, Massac Co. (USNM). Ohio River, Shawneetown, Gallatin Co. (MCZ).

Wabash River Drainage. *Illinois:* Wabash River, 2 mi. W Maunie, White Co. (Parmalee). *Indiana:* Wabash River, New Harmony, Posey Co. (MCZ). *Illinois:* Wabash River, Grayville, White Co. (USNM). *Indiana:* White River, Hazleton, Gibson Co. (MZUM). West Fork, White River, Strawtown, Hamilton Co. (MZUM).

St. Lawrence River System

Great Lakes Drainage (Lake Erie). *New York:* Niagara River, Buffalo, Erie Co. (Lake Ontario). *New York:* Wilson's Creek [= Twelvemile Creek, near Wilson], Niagara Co. These records (Robertson and Blakeslee 1948: 106) are based on specimens in the Buffalo Museum of Science, which have been examined and are authentic.

Genus *Villosa* Frierson

Micromya Agassiz 1852, Archiv für Naturgeschichte, **18** (1): 47. Type species, *Unio lapillus* Say, subsequent designation, Herrmannsen, 1852, Indicis Generum Malacozoorum, Supp. et Corr., p. 83, *non Micromya* Rondani 1840 (Insecta).

Villosa Frierson 1927, Check list N American naiades, pp. 11, 80. Type species, *Unio villosus* Wright, original designation.

Villosa arkansasensis (Lea)

Plate 16, figures 3, 4
Distribution: Plate 8 A

Unio arkansasensis Lea 1862, Proc. Acad. Nat. Sci. Phila. **14:** 169 ([Ouachita River] near Hot Springs, [Garland Co.], Arkansas); 1862, Jour. Acad. Nat. Sci. Phila. (2) **5:** 206, pl. 30, fig. 275, figured holotype USNM 25710; Obs. Unio **9:** 28. Call, 1895, Trans. Acad. Sci. St. Louis **7:** 6.

Lampsilis arkansasensis (Lea). Simpson, 1900, Proc. U. S. Natl. Mus. **22:** 557; 1914, Cat. Naiades **1:** 130.

Eurynia (*Micromya*) *arkansasensis* (Lea). Ortmann, 1916, Nautilus **30:** 54. Wheeler, 1918, Nautilus **31:** 118.

Description. Shell small in size, seldom exceeding 40 mm in length. Outline ovate, or short obovate. Valves subinflated, solid. Anterior end regularly rounded; posterior end somewhat pointed. Ventral margin regularly curved. Dorsal margin rather rounded, forming a more or less distinct angle with the obliquely descending posterior margin. Posterior ridge, low, almost double, ending a slight biangulation below the medial line. Hinge ligament short. Umbos not much swollen, slightly projected above the hinge line, the sculpture not observed, located in the anterior third of the shell. Surface of the shell with irregularly concentrical striations. Periostracum dull to subshiny, yellowish to brownish, usually with fine green rays over the entire surface.

Left valve with two rather heavy, triangular, pseudocardinal teeth of about equal size, and two short lateral teeth. Right valve with two pseudocardinals, the posterior one chunky, the more anterior tooth vestigial. No interdentum. One lateral tooth. Anterior adductor muscle scars well impressed, posterior ones faint. Pallial line visible anteriorly. Nacre silvery white, bluish, iridescent posteriorly.

Male shells are somewhat pointed. Female shells are more broadly rounded, and truncated below the medial line. In mature females there is a distinct "constriction" in the middle of this truncation.

Length mm	Height mm	Width mm	
40	28	18	[Ouachita River], Hot Springs, [Garland Co.], Arkansas. Holotype. Male.
38	27	18	Saline River, Benton, Saline Co., Arkansas. Female.

Anatomy and Breeding Season. The anatomy was discussed by Ortmann (1916, Nautilus **30:** 54).

Remarks. Villosa arkansasensis (Lea) is most closely related to the Cumberlandian species, *V. vanuxemensis vanuxemensis* (Lea). Shells of the former are more swollen, less elongate, and the umbos are located more anteriorly. Further, in females the enlarged and truncated posterior end is more evenly rounded, and not as produced as it is *V. v. vanuxemensis*. The periostracum of *arkansasensis* is usually yellowish to brownish and rayed. The nacre is always white. The periostracum of *vanuxemensis* is from dirty tawny through olive to nearly black, and is not always rayed. The nacre is very rarely white. It is usually dirty purplish-white, through salmon-tinted to dark purple. The most important similarity between the two species is the characteristic "constriction" on the posterior truncation of the female shells.

Range. Found only in the Ozarkian Region, below the Ozark Crest, in the upper Black River System.

Abundance. Never taken in large numbers.

Specimens Examined

Black River System

Ouachita River Drainage. *Arkansas:* Ouachita River, 3 mi. S.E. Pencil Bluff, Montgomery Co. (MCZ); Ouachita River, near Hot Springs, Garland Co. (USNM); Ouachita River, S Arkadelphia, Clark Co. (Wheeler).

Little Missouri River Drainage. *Arkansas:* Little Missouri River, Murfreesboro, Pike Co. (MZUM).

Caddo River Drainage. *Arkansas:* Caddo River (MZUM).

Saline River Drainage. *Arkansas:* Saline River, Benton (MCZ, MZUM); 3.5 mi. SE Traskwood (MCZ); *both* Saline Co.

Villosa reeviana (Lea)

Plate 17, figures 1–5

Distribution: Plate 7 B

Unio reevianus Lea 1852, Trans. Amer. Philos. Soc. **10:** 272, pl. 20, fig. 28 (Alexandria, Louisiana [erroneous]; holotype USNM 85025 male; paratype MCZ 178918 male, labeled, "Arkansas. Lea so decided from this specimen and another, Powell."; allotype USNM 85025a, labeled, "White River, Arkansas." The type locality is here restricted to: White River, Elkins, Washington Co., Arkansas); 1852, Obs. Unio **5:** 28.

Unio breviculus Call 1887, Proc. U. S. Natl. Mus. **10:** 499, pl. 28 (Currant [Current] River, Shannon Co., Missouri and in Jacks Fork and Big Creek, tributaries to it; lectotype selected by Johnson, 1975, Occ. Papers on Moll. **4** (54): 141, MCZ 5020, male specimen portrayed in figs. 1, 1a, 1b, from Jacks Fork [Shannon Co.]; figured allotype MCZ 5023 portrayed in figs. 2, 2a, 2b, from Big Creek [Fork], Texas Co.); 1895, Trans. Acad. Sci. St. Louis **7:** 6, pl. 17.

Lampsilis brittsi Simpson 1900, Proc. Acad. Nat. Sci. Phila. **52:** 76, pl. 5, figs. 1–2 (no locality [Niangua River, Camden Co., Missouri]; holotype USNM 152700).

Lampsilis reeviana (Lea). Simpson, 1914, Cat. Naiades **1:** 74. Utterback, 1916, Amer. Midl. Nat. **4:** 449 [186]. Frierson, 1927, Check list N American naiades, p. 73.

Lampsilis brevicula (Call). Simpson, 1914, Cat. Naiades, **1:** 57. Ortmann, 1918, Nautilus **32:** 14.

Eurynia (*Micromya*) *brevicula* (Call). Utterback, 1916, Amer. Midl. Nat. **4:** 434 [171], pl. 27, figs. 98 A–D.

Lampsilis reeviana brevicula (Call). Frierson 1927, Check list N American naiades, p. 73.

Lampsilis breviculus brittsi Simpson. 1900. Proc. U. S. Natl. Mus. **22:** 533. 1914, Cat. Naiades **1:** 58.

Eurynia (*Micromya*) *brevicula brittsi* (Simpson). Utterback, 1916, Amer. Midl. Nat. **4:** 435 [172], pl. 27, figs. 99 A, B.

Description. Shell of medium size, not exceeding 80 mm in length. Outline ovate, elliptical or obovate. Valves subinflated, rather thin to subsolid, inequilateral. Anterior end regularly rounded, posterior end more broadly rounded. Ventral margin slightly curved. Dorsal margin somewhat curved, forming a barely perceptible angle with the obliquely descending posterior margin. Hinge ligament is long, passing under the umbos and appearing anteriorly in front of a small lunule. Posterior ridge indistinct. Umbos are not very full, but slightly elevated above the hinge line, their sculpture not observed, located very anteriorly. Surface of the shell is smooth. Periostracum is generally shiny or subshiny, greenish straw color, having a smoky tint, or yellowish horn-color, with dark green rays, generally over the entire surface. The rays are usually delicate, and generally broken.

Left valve with two delicate, subcompressed pseudocardinal teeth. These are located anterior of the umbo, with the more anterior tooth being the higher. Of the two lateral teeth present, the inner tooth is the higher. Right valve with a somewhat compressed pseudocardinal tooth, with a smaller one above it separated by a deep, parallel-sided pit, often with the vestige of another tooth behind. Interdentum is very narrow and curved. One lateral tooth is truncate posteriorly. Muscle scars and umbonal cavities are shallow, pallial line only visible anteriorly. Nacre is whitish, pinkish, bluish white.

Male shells are quite elliptical, and faintly biangulate posteriorly. Female shells are shorter and higher than those of the male and strongly inflated post-basally. The low posterior ridge ends in a decided point about three-fifths of the way up from the base. The post-basal margin appears truncated. This truncation may be slightly to considerably emarginate.

Length mm	Height mm	Width mm	
75	41	28	[Arkansas] Holotype of *U. reevianus*. Male.
62	39	23	White River, Arkansas. Allotype of *U. reevianus*. Female.
64	40	24	Jacks Fork, Current River, Shannon Co., Missouri. Lectotype of *U. breviculus*. Male.

58	40	25	Big Fork, Current River, Texas Co., Missouri. Allotype of *U. breviculus*. Female.

Anatomy and Breeding Season. The anatomy was discussed by Call (1887, Proc. U. S. Natl. Mus. **10:** 499) and by Ortmann (1918, Nautilus **32:** 15), on the basis of which, the latter placed *U. breviculus* under *Lampsilis*. A glochidium was figured by Surber (1915, pl. 1, fig. 14) as *L. b. brittsi*, 0.23 × 0.29. Breeding season not recorded.

Habitat. Found by Call in shallow mountain streams, "being swift and limpid, with rocky bottoms."

Remarks. Villosa reeviana (Lea), as pointed out by Call, does not much resemble any other Ozarkian species. There is some variation within the several populations as to the thickness of the shell, width of the rays and degree of sexual dimorphism in the female. The male shell of *V. reeviana* has been confused with specimens of *V. vibex* (Conrad). The latter has a consistently thinner shell, broader green rays, and the female differs from the male only in that the posterior end of the shell is more broadly rounded, the post-basal margin is not truncated. The specimens mentioned by Frierson (1927: 74) from Onion Creek, Travis Co., Texas MZUM 79921 are *vibex*.

Range. Found only in the Ozarkian Region: below the Ozark Crest in the White River system; and above it in the Meramec, Gasconade and Osage River systems.

Abundance. Taken in large numbers from several localities in the Meramec River system by the Harvard-Ohio State Museum Expedition in 1965.

Specimens Examined

White River System

White River Drainage. *Arkansas:* Main Fork White River, Elkins, Washington Co. (MCZ). *Missouri:* James River, Galena, Stone Co. (MCZ, MZUM); White River, Hollister and Forsyth (*both* MZUM), *both* Taney Co. *Arkansas:* White River, Cotter (MZUM) and Norfolk (MCZ), *both* Baxter Co.

Big Buffalo Fork Drainage. *Arkansas:* Big Buffalo Fork, near Gilbert, Searcy Co.; Big Buffalo River, Buffalo River State Park, Marion Co.; (*both* MZUM).

Current River Drainage. *Missouri:* Big Creek, Texas Co.; Jacks Fork; Current River between Eminence and Ellsinore; *both* Shannon Co.; Current River, Big Spring State Park, Carter Co.; Current River, 1 mi. SW Doniphan, Ripley Co.; Eleven Point River, Riverton, Oregon Co.; (*all* MCZ).

Black River Drainage. *Missouri:* Mill Creek, 1 mi. E Lesterville, Reynolds Co. (MZUM).

Spring River Drainage. *Arkansas:* Spring River, Salem, Fulton Co. (MCZ).

Meramec River System

Big River Drainage. *Missouri:* Cedar Creek (MZUM), Mineral Fork, *both* Washington Co.; Big River, Jefferson Co. (*both* Buchanan, 1977, p. 31).

Meramec River Drainage. *Missouri:* Huzzah Creek, Crawford Co. (MZUM); Meramec River, Dent Co.; Meramec River, Steelville, Crawford Co. (*both* MCZ); Meramec River, at Franklin and St. Lewis Co. line (Buchanan, 1977, p. 31).

Bourbeuse River Drainage: *Missouri:* Bourbeuse River, Franklin Co. (Buchanan, 1977, p. 31).

Gasconade River System

Gasconade River Drainage. *Missouri:* Big Piney River, 7 mi. W Licking, Texas Co.; Gasconade River, 6 mi. NW Vichy, Maries Co. (*both* MCZ).

Osage River System

Osage River Drainage. *Missouri:* Little Niangua River (MCZ, MZUM); Niangua River, Hahatonka (Utterback); *both* Camden Co.

Genus *Cyprogenia* Agassiz

Cyprogenia Agassiz 1852, Archiv für Naturgeschichte, **18** (1): 47. Type species, *Unio irroratus* Lea, original designation. Ortmann, 1912, Ann. Carnegie Mus. **8**: 312.

Cyprogenia aberti (Conrad)

Plate 19, figure 3
Plate 20, figures 1–4
Distribution: Plate 6

Unio aberti Conrad 1850, Proc. Acad. Nat. Sci. Phila. **5**: 10 (Rapids of Verdigris River, Chambers' Ford [not located, Oklahoma] Arkansas [River system]; 1854, Jour. Acad. Nat. Sci. Phila. (2) **2**: 295, pl. 26, fig. 1, figured type not located by Johnson and Baker, 1973, Proc. Acad. Nat. Sci. Phila. **125**: 147. Call, 1895, Trans. Acad. Sci. St. Louis **7**: 4.

Unio lamarckianus Lea 1852, Trans. Amer. Philos. Soc. **10**: 266, pl. 17, fig. 20 (Caddo River; Washita [Ouachita] River, near the Hot Springs, [Garland Co.]; *both* Arkansas; figured holotype USNM 84306, labeled, "White River, Arkansas."); 1852, Obs. Unio **5**: 22.

Unio popenoi Call 1885, Bull. Washburn College Lab. Nat. Hist. **1**: 49, pl. 2 (Fall River, Wilson Co., figured holotype MCZ 4934; Verdigris River; *both* Kansas); is *Unio aberti* Conrad, *teste* Call, 1887, Amer. Nat. **21**: 860.

Cyprogenia aberti (Conrad). Seammon, 1906, Kansas Univ. Sci. Bull. **3**: 315, pl. 71, fig. 2. Simpson, 1914, Cat. Naiades **1**: 328. Utterback, 1916, Amer. Midl. Nat. **4**: 322 [134], pl. 25, figs. 83 A, B. Isely, 1925, Proc. Oklahoma Acad. Sci. **4**: 103. Murray and Leonard, 1962, Univ. Kansas, Mus. Nat. Hist., Pub. no. 28, p. 105, pl. 27, figs. 1–4, text fig. 23. Branson, 1966, Sterkiana no. 23, p. 7.

Cyprogenia aberti lamarckiana (Lea). Simpson, 1914, Cat. Naiades, **1**: 329. Utterback, 1916, Amer. Midl. Nat. **4**: 323 [135].

Unio irroratus Call. 1895, Trans. Acad. Sci. St. Louis **7**: 20, *non* Lea 1828.

Description. Shell of medium size, seldom exceeding 80 mm in length. Outline usually rhomboidal, occasionally rounded triangular. Valves slightly inflated, thick and heavy. Anterior end regularly rounded; posterior end subtruncate. Ventral margin more or less rounded, tending to be straight or slightly concave posteriorly. Dorsal margin slightly convex forming a more or less distinct angle with the almost vertical, sometimes concave, posterior margin. Hinge ligament rather long. Posterior ridge well developed, high and narrow at the umbonal region, becoming flattened and somewhat double, with a wide shallow groove before it. Posterior slope with a radial furrow, very narrow. Umbos low and compressed, curved forward over the lunule, located at the middle of the shell or somewhat anteriorly. Surface of the shell with strong, low, more or less numerous, concentric ridges; in addition it is sometimes subvertically wrinkled and nodulous. Periostracum scarcely shining, yellowish green, with dots and flecks of dark green which fall into broad broken rays. Hinge very broad and flat. Left valve with two heavy, triangular, blunt and ragged, pseudocardinal teeth of about equal height; also with two short, very low lateral teeth. Right valve with one large pseudocardinal, sometimes with a feeble one on each side of it. Interdentum is very broad. One low double or triple lateral tooth. Umbonal cavities are very shallow and compressed. Anterior and posterior adductor muscle scars and pallial line are all well impressed. Nacre is white, thinner and somewhat iridescent anteriorly.

Length mm	Height mm	Width mm	
80	75	44	Fall River, Wilson Co., Kansas. Paratype of *Unio popenoi.*
48	41	26	Ouachita River, Arkadelphia, Clark Co., Arkansas.

Anatomy and Breeding Season. Unknown.

Habitat. Reported from Kansas as living in rocky, gravel or soft mud substrates (Murray and Leonard, 1962: 107).

Remarks. Cyprogenia aberti (Conrad) of the Ozarkian Region is readily distinguishable from all other unionids there by the peculiar, mottled color of the periostracum; its generally compressed, oval or rhomboidal shell; and by the subvertical wrinkles or nodules which occur at least on the upper part of the disk. While most specimens of *aberti* are oval or rhomboidal, some specimens become

rounded triangular, much resembling *C. stegaria* of the Cumberlandian and Ohioan regions. Call (1895: 20) in a collection made in the St. Francis River, Wittsburg, Cross Co., Arkansas, noted that many of the young appeared to be *aberti*, but that, "the triangular outline is lost with age and the circular form becomes more and more marked." This lot, MCZ 5492, now consists of only two adult specimens. He also mentioned specimens from the Saline River of the Black River system, now lost. He regarded both of these lots as being *irroratus* = *stegaria*. Frierson (1927: 66) mentioned that *stegaria* and *aberti* "almost merge into one unbroken chain in the state of Arkansas." Having studied virtually all of the available material, it is admitted that occasional specimens of both *aberti* and *stegaria* closely resemble one another, but the shell of the former species always has a much narrower, and more compressed posterior slope.

Range. Found only in the Ozarkian Region: below the Ozark Crest in the Black, Arkansas, White, and St. Francis river systems; and above it in the Meramec River system.

Abundance. Formerly abundant in the Fall River, Kansas. Murray and Leonard (1962: 107) claimed that this species has not been collected in Kansas since 1906. Collected in some numbers by the Harvard-Ohio State Museum Expedition, 1965, in the Ouachita River, of the Black River system, near Pencil Bluff, Montgomery Co., Arkansas.

Specimens Examined

Ozarkian Region

Black River System

Ouachita River Drainage. *Arkansas:* Ouachita River, 3 mi. SE Pencil Bluff, Montgomery Co. (MCZ); Ouachita River, nr. Hot Springs, Garland Co. (Lea); Ouachita River, N Cove Creek, Hot Springs Co. (CM); Caddo Creek (USNM); Ouachita River, Arkadelphia, Clark Co. (MCZ).

Saline River Drainage. *Arkansas:* Saline River, Benton, Saline Co. (MCZ).

Arkansas River System

Verdigris River Drainage. *Kansas:* Fall River, 3.5 mi. S Fredonia, Wilson Co. (MZUM); Verdigris River (MCZ). *Oklahoma:* Verdigris River, Oologa (USNM), Catoosa, NW Inola (*both* Isely), *all* Rogers Co. Verdigris River, Chambers Ford [not located] (Conrad).

Neosho River Drainage. *Kansas:* Neosho River, Lyon Co. (Murray and Leonard); Spring River, 2 mi. E Pittsburg (Branson).

White River System

White River Drainage. *Arkansas:* White River, Elkins, Washington Co. (MCZ). *Missouri:* White River, Hollister (Utterback), Forsyth (MZUM), *both* Taney Co. *Arkansas:* White River, Cotter, Norfork (*both* MCZ), *both* Baxter Co.

Big Buffalo Fork Drainage. *Arkansas:* Big Buffalo Fork, Newton Co. (Meek and Clark); Big Buffalo Fork, 2.5 mi. below Red Cloud Mine, Marion Co. (MZUM, from Meek and Clark, Station 25).

Little Red River Drainage. *Arkansas:* Little Red River, Clinton, Van Buren Co. (MCZ).

Black River Drainage. *Missouri:* Black River, .5 mi. W Hendrickson (MCZ), Poplar Bluff (MZUM), *both* Butler Co. *Arkansas:* Black River, Pocahontas, Randolph Co. (MCZ).

Spring River Drainage. *Arkansas:* South Fork Spring River nr. Salem, Fulton Co. (MZUM); Spring River, Hardy, Sharp Co.; Spring River, Black Rock, Lawrence Co. (*both* MCZ).

St. Francis River System

St. Francis River Drainage. *Missouri:* Little St. Francis River, 9 mi. E Ironton, Madison Co. (MZUM); St. Francis River, Greenville, Wayne Co. (MZUM); St.

sas: Tyronza River, Tyronza, Poinsett Co. (MZUM); St. Francis River, Wittsburg, Cross Co. (MCZ).

Meramec River System

Meramec River Drainage. *Missouri:* Meramec River, Crawford Co. (see Plate 20 fig. 4)

Cyprogenia stegaria (Rafinesque)

Plate 18, figures 1, 2
Plate 19, figures 1, 2
Distribution: Plate 6

Obovaria stegaria Rafinesque 1820, Ann. Gén. Sci. Physiques, Bruxelles **5:** 308 (l'Ohio [River]; lectotype ANSP 20215, selected by Johnson and Baker, 1973, Proc. Acad. Nat. Sci. Phila. **125:** 173, pl. 4, fig. 3).

Unio verrucosus albus Hildreth 1828, Amer. Jour. Sci. **14:** 281 (Muskingum [River, near Marietta, Washington Co., Ohio]; type [lost]).

Unio irroratus Lea 1828, Trans. Amer. Philos. Soc. **3:** 269, pl. 5, fig. 5 (Ohio; figured holotype USNM 84637 [lost]. Reeve, 1864, Conch. Iconica **16:** *Unio*, pl. 12, species 44).

Cyprogenia irrorata pusilla Simpson 1900, Proc. U. S. Natl. Mus. **22:** 610 (Green River [Mammoth Cave, Edmonson Co.] Kentucky; lectotype USNM 152004, selected by Johnson, 1975, Special Occ. Pub., Dept. Moll., Mus. Comp. Zool. no. 4: 17; pl. 2, fig. 2).

Unio stegarius (Rafinesque). Say, 1834, Amer. Conch. no. 6 [no pagination] *Unio irroratus* Lea is listed as a synonym. Conrad, 1838, Monography Unionidae of North America, no. 10, p. 83, pl. 46, fig. 1. Reeve, 1864, Conch. Iconica **16:** *Unio*, pl. 12, species 45.

Cyprogenia stegaria (Rafinesque). Ortmann, 1919, Mem. Carnegie Mus. **8:** 218, pl. 13, fig. 5. Frierson, 1927, Check list N American naiades, p. 66.

Cyprogenia irrorata (Lea). Simpson, 1900, Proc. U. S. Nat. Mus. **22:** 610. Ortmann, 1912, Ann. Carnegie Mus. **8:** 312, fig. 17. Simpson, 1914, Cat. Naiades **1:** 327. Ortmann and Walker, 1922, Occ. Papers, Mus. Zool., Univ. Michigan no. 112, p. 43. La Rocque, 1967, Geol. Surv. Ohio, Bull. No. 62 (2): 232, figs. 118, 119. Parmalee, 1967, Illinois State Mus., Popular Sci. Ser. **8:** 61, pl. 20: A, Frontispiece.

Description. Shell of medium size, seldom exceeding 80 mm in length. Outline subcircular, subtrapezoidal, or rounded triangular. Valves somewhat inflated, thick and heavy. Anterior end broadly rounded; posterior end subtruncate. Ventral margin more or less rounded, tending to be straight or slightly concave posteriorly. Dorsal margin slightly convex, forming an angle with the almost vertical posterior margin. Hinge ligament rather long. Posterior ridge well developed, high and narrowly rounded at the umbonal region; with a radial groove anterior to it and another shallower one posterior to it. Posterior slope slightly concave or flattened, rather broad. Umbos moderately high and full, but flattened, curved forward over the lunule, their sculpture consisting of a few slightly double-looped bars, located at the middle of the shell or somewhat anteriorly. Surface of the shell with strong, low, more or less numerous concentric ridges, The anterior end may be smooth, but there are usually nodules elsewhere where they assume a radial pattern. The nodules may be missing in older specimens. Periostracum light green or yellow, to light brown, ornamented with green mottlings, which fall into fine or broad green rays.

Hinge well developed. Left valve with two heavy, triangular, blunt and ragged, pseudocardinal teeth of about equal height, two short heavy lateral ones. Right valve with one large pseudocardinal. Interdentum very broad and short. One strong double lateral tooth. Umbonal cavities shallow, and compressed. Anterior and posterior adductor muscle scars and pallial line all well impressed. Nacre silvery white, seldom bluish or pinkish.

Length mm	Height mm	Width mm	
64	64	44	Tuscarawas River, New Philadelphia, Tuscarawas Co., Ohio.
49	49	35	Clinch River, Clinton, Anderson Co., Tennessee.

Anatomy and Breeding Season. Ortmann (1919: 219) discussed the several anatomical descriptions. A glochidium was figured by Ortmann (1912: pl. 19, fig. 6) and by Surber (1912: pl. 1, fig. 11). Ac-

cording to Ortmann it measured 0.18 × 0.15. He also (1919: 219) indicated that this species is bradytictic.

Habitat. Found in firmly packed gravel, in strongly flowing water in the Clinch and Holston rivers and in mussel beds on gravelly bottoms with steady currents in the deep channel of the Ohio River between Cincinnati and Pittsburgh (Ortmann, 1919: 220).

Remarks. In the Cumberlandian and Ohioan regions, *Cyprogenia stegaria* (Rafinesque) is distinguishable from all other unionids by the peculiar, mottled character of the color of the periostracum, and by its generally subglobular shape and nodular surface, although the shape and development of the nodules is variable. Occasional specimens resemble *C. aberti* (Conrad) of the Ozarkian Region (see Remarks under this section).

Specimens from the Cumberlandian Region are, in general, not as large as those from the Ohioan Region. *C. stegaria* appears to have found a more favorable environment in the Ohioan Region in post-glacial time, as apparently did *Plagiola flexuosa* (Rafinesque) (Johnson 1978: 284).

As indicated in the synonymy, Rafinesque's name for this species has been used by Say, Conrad, Ortmann, Frierson and others. Ortmann and Walker (1922: 43) argued that this species could not be identified from Rafinesque's description alone. Frierson (1927: 66) indicated that it could be so identified. The present *Rules of International Nomenclature* (1964) emphasize the identification of the type, so Rafinesque's name is clearly available.

Range. Cumberlandian Region: Tennessee and Cumberland river systems. Ohioan Region: Ohio River and its tributaries.

Abundance. This species appears to be locally abundant.

Specimens Examined

Cumberlandian Region

Tennessee River System

Clinch River Drainage. *Virginia:* Clinch River, Clinchport, above mouth of Copper Creek, 1.5 mi. below Speers Ferry bridge, *all* Scott Co.; Clinch River, 1.5 mi. S Dona, Lee Co. (*all* MCZ). *Tennessee:* Clinch River, below Kyles Ford bridge, Hancock Co. (MCZ); Clinch River, Clinch River Station, Claiborne Co. (CM); Clinch River, 4 mi. NW Thorn Hill, Grainger Co.; Clinch River, Clinton and Edgemoor, *both* Anderson Co.; Clinch River, 3 mi. S Wheat, Roane Co. (*all* MCZ).

Holston River Drainage. *Tennessee:* Holston River, Turley Mill, Grainger Co. (CM); Holston River, Mascot and near Knoxville, *both* Knox Co. (*both* MCZ).

Tennessee River Drainage. *Tennessee:* Tennessee River, Knoxville, Knox Co. (MCZ); Tennessee River, Rathburn, Hamilton Co. (MZUM). *Alabama:* Tennessee River, Bridgeport, Jackson Co. (MCZ).

Flint River Drainage. *Alabama:* Flint River [Madison Co.] (MZUM).

Tennessee River Drainage. *Alabama:* Tennessee River, Florence, Lauderdale Co.; Tennessee River, Tuscumbia, Colbert Co. (*both* MCZ); Pickwick Basin, mounds between Barton, Colbert Co. and Waterloo, Lauderdale Co. (Morrison).

Duck River Drainage. *Tennessee:* Duck River, Columbia, Maury Co. (Hinkley and Marsh, single specimen).

Cumberland River System

Cumberland River Drainage. *Kentucky:* Cumberland River, below Wolf Creek Dam, Russell Co. (MCZ); Cumberland River, Albany Landing; Cloyds Landing; *both* Cumberland Co.; (*both* CM).

Obey River Drainage. *Tennessee:* Obey River, Duncan Ford, 4 mi. SE Lilydale, Pickett Co. (MCZ).

Cumberland River Drainage. *Tennessee:* Cumberland River, Goodall Island, Smith Co. (Wilson and Clark); Cumber-

Francis River, Butler Co. (MCZ). *Arkan-*land River, Nashville, Davidson Co. (MCZ).

Ohioan Region

Ohio River System

Wabash River Drainage. *Indiana:* Wabash River, New Harmony, Posey Co.; Wabash River, Mt. Carmel, Wabash Co.; Wabash River, Terre Haute, Vigo Co.; Wabash River, Lafayette, Tippecanoe Co.; Wabash River, Delphi, Carroll Co.; Wabash River, Tippecanoe River, *both* White Co.; (*all* MCZ).

White River Drainage. *Indiana:* White River (MCZ).

Green River Drainage. *Kentucky:* Green River, Rio, and Munfordville, *both* Hart Co. (*both* MCZ); Green River, Mammoth Cave (MCZ); Onyx Cave (CM); *both* Edmonson Co.; Barren River, Bowling Green, Warren Co.; Green River, below dam at Rochester, Muhlenberg Co. (*both* MCZ).

Salt River Drainage. *Kentucky:* Rolling Fork, Salt River, .5 mi. S New Haven, Nelson Co. (MCZ).

Kentucky River Drainage. *Kentucky:* Kentucky River (Danglade).

Licking River Drainage. *Kentucky:* Licking River, Butler, Pendleton Co. (MCZ).

Ohio River Drainage. *Ohio:* Great Miami River (Sterki); Ohio River, Cincinnati, Hamilton Co. (MCZ); Little Miami River, Xenia, Green Co. (CM); Scioto River (MCZ); Ohio River, Portsmouth, Scioto Co. (CM): *Virginia:* Big Sandy River (MCZ). *Ohio:* Ohio River, Portland, Meigs Co. (CM). *West Virginia:* Ohio River, Parkersburg, Wood Co. (CM).

Muskingum River Drainage. *Ohio:* Muskingum River, Lowell, Washington Co.; Tuscarawas River, New Philadelphia, Tuscarawas Co.; (*both* MCZ).

Ohio River Drainage. *West Virginia:* Ohio River, St. Marys, Pleasants Co. (CM); Ohio River, Clarington, Monroe Co. (MCZ). *Pennsylvania:* Ohio River, Industry, Beaver Co. (CM).

Big Beaver River Drainage. *Ohio:* Mahoning River (Sterki).

Allegheny River Drainage. *Pennsylvania:* Allegheny River, Godfrey and Alladin, *both* Armstrong Co. (*both* CM); Allegheny River, Natrona, Allegheny Co. (CM).

Monongahela River Drainage. *Pennsylvania:* [Monongahela River] Indian kitchen-midden opposite Point Marion, Fayette Co. (CM).

Genus *Ptychobranchus* Simpson

Ptychobranchus Simpson 1900, Proc. Acad. Nat. Sci. Phila. **52:** 79. Type species, *Unio phaseolus* Hildreth, original designation. Ortmann, 1912, Ann. Carnegie Mus. **8:** 305.

Subtentus Frierson 1927, Check list N American naiades, pp. 10, 65. Type species, *Unio subtentus* Say, original designation. Frierson created this monotypic subgenus for *P. subtentum* (Say), a Cumberlandian species, probably because of the corrugations on its posterior slope. Its use seems unnecessary in a genus consisting of 4 species. In addition to *P. subtentum*; there is *fasciolare* (Rafinesque) from the Cumberland and Ohioan Regions; *occidentalis* (Conrad) from the Ozarkian Region; and *greeni* (Conrad) which is restricted to the Mobile-Alabama-Coosa River system.

Ptychobranchus occidentalis (Conrad)
Plate 20, figures 5, 6
Distribution: Plate 7 A

Unio occidentalis Conrad 1836, Monography Unionidae, no. 7, p. 64, pl. 36, fig. 1 (Current River [Randolph Co.], Arkansas, figured type not located, *teste*, Johnson and Baker, 1973, Proc. Acad. Nat. Sci. Phila. **125:** 163).

Ptychobranchus clintonensis Simpson 1900, Proc. Acad. Nat. Sci. Phila. **52:** 79, pl. 5, fig. 3 (Archies Fork of Little Red River, near Clinton [Van Buren Co.], Arkansas; holotype USNM 124615); 1900, Proc. U. S. Natl. Mus. **22:** 613; 1914, Cat. Naiades **1:** 335. Isely, 1925, Proc. Oklahoma Acad. Sci. **4:** 102.

Ellipsaria clintonensis (Simpson). Utterback, 1916, Amer. Midl. Nat. **4:** 316 [128], pl. 25, figs. 81 A, B.

Ptychobranchus occidentalis (Conrad). Valentine and Stansbery 1971, Sterkiana, no. 42, p. 23.

Ptychobranchus phaseolus Scammon. 1906, Univ. Kansas Sci. Bull. **3:** 319, pl. 72, fig. 2. Isely, 1925, Proc. Oklahoma Acad. Sci. **4:** 102; *non* Hildreth 1828.

Ptychobranchus fasciolare Murray and Leonard. 1962, Univ. Kansas, Mus. Nat. Hist., Pub. no. 28, p. 162, pl. 45, fig. 1, *non* Rafinesque 1820.

Description. Shell medium to large, occasionally exceeding 100 mm in length. Outline oblong, ovate, elliptical or subrhomboid, sometimes subtriangular. Valves subinflated, very solid. Anterior end regularly rounded. Posterior end more broadly rounded. Ventral margin straight or slightly curved. Dorsal margin curved imperceptably joining the obliquely descending posterior margin. Hinge ligament long. Posterior ridge usually indistinct, rounded, often somewhat double, ending in a slight biangulation near the base. Umbos not inflated, or much raised above the hinge line, their sculpture not seen, located considerably forward of the middle of the shell. Surface of the shell smooth. Periostracum yellowish-green, brownish, with very delicate, wavy, continuous green rays, often over the entire surface.

Left valve with two low, small, solid, pseudocardinal teeth, and two low lateral teeth. Right valve with one large tooth directly under the umbo, with a vestigial one on either side of it. Interdentum short but very wide. One lateral tooth which is sometimes more or less double. Umbonal cavities very shallow; anterior and posterior muscle scars well impressed. Pallial line impressed anteriorly. Nacre bluish white, often with lurid blotches.

Length mm	Height mm	Width mm	
116	67	40	Verdigris River, Neodesha, Wilson Co., Kansas.
91	45	27	Archies Fork, of Little Red River, nr. Clinton, Van Buren Co., Arkansas. Paratype of *P. clintonensis* MCZ 192371.

Anatomy and Breeding Season. Discussed in part under *P. phaseolus* (Hildreth), by Ortmann (1912: 306). *P. occidentalis* is bradytictic.

Remarks. Ptychobranchus occidentalis (Conrad) is restricted to the Ozarkian Region. It is most closely related to *P. fasciolare* (Rafinesque) of the Cumberlandian and Ohioan regions. Valentine and Stansbery (1971: 23) claimed to have specimens of *fasciolare* from Missouri, and while their specimens were not examined, all other specimens studied from Missouri proved to be *occidentalis*. While *occidentalis* and *fasciolare* are very similar, most of the rays on the shell of the former are always very fine, uniform, and generally continuous, while those of the latter are always wide, and often broken into spots.

In the Ozarkian Region *occidentalis* has been confused with *Elliptio dilatata* (Rafinesque). It does not much resemble the latter which has a longer, less high shell, often with an arcuate ventral margin. It is seldom rayed, and usually has a violet nacre.

Range. Found only in the Ozarkian Region: below the Ozark Crest in the Red, Black, Arkansas, White, and St. Francis river systems; and above it in the Meramec River system.

Abundance. The size of the lots examined tend to indicate this species is rather abundant.

Specimens Examined

Red River System

Blue River Drainage. *Oklahoma:* Blue River, Milburn, Johnson Co.; Blue River, Durant, Bryan Co.; (*both* Valentine and Stansbery, 1971: 23).

Kiamichi River Drainage. *Oklahoma:* Kiamichi River, Tuskahoma, Pushmataka Co. (MZUM).

Little River Drainage. *Oklahoma:* Glover Creek, Glover, McCurtain Co. (MCZ). *Arkansas:* Cossatot River, 5.5 mi. ESE Gillham; Rolling Fork River, S Gillham; *both* Sevier Co. (*both* MCZ).

Black River System

Ouachita River Drainage. *Arkansas:* Ouachita River, 3 mi. SE Pencil Bluff, Montgomery Co.; Ouachita River, Arkadelphia, Clark Co. (*both* MCZ); Ouachita River, Camden, Ouachita Co. (MZUM).

Caddo Creek Drainage. *Arkansas:*

Caddo Creek, Caddo Gap, Montgomery Co.; Caddo Creek, 4 mi. above mouth, Caddo Valley, Clark Co.; (*both* MCZ).

Saline River Drainage. *Arkansas:* Saline River, Benton, Saline Co.; Saline River, Jenkins Ferry, Grant Co.; (*both* MZUM).

Arkansas River System

Verdigris River Drainage. *Kansas:* Fall River, Elk Co.; Verdigris River, Neodesha, Wilson Co.; (*both* MCZ).

Neosho River Drainage. *Kansas:* Neosho River, Iola, Allen Co. (MCZ, MZUM). *Missouri:* Spring River, Carthage (MCZ) and Webb City (Utterback); *both* Jasper Co. *Kansas:* Spring River, Cherokee Co. (Branson, 1966, Nautilus **80:** 22).

White River System

White River Drainage. *Arkansas:* White River, Sulphur City and N Elkins (*both* MZUM), *both* Washington Co. *Missouri:* James River, Galena, Stone Co. (MCZ); White River, Hollister (Utterback), Forsyth (MZUM); *both* Taney Co. *Arkansas:* White River, Cotter (MCZ) and Norfolk (MZUM), *both* Baxter Co.; Archie's Fork, Little Red River, near Clinton, Van Buren Co. (MCZ).

Black River Drainage. *Missouri:* Black River, Poplar Bluff, Butler Co. (MCZ).

Spring River Drainage. *Arkansas:* South Fork Spring River, near Salem, Fulton Co.; Spring River, Hardy and Willford; *both* Sharp Co.; Spring River, Black Rock, Lawrence Co.; (*all* MZUM).

Current River Drainage. *Missouri:* Big Creek, Texas Co. (MCZ, MZUM); Jacks Fork, Shannon Co. (Utterback); Current River, Big Spring State Park, Carter Co. (MZUM); Current River, 1 mi SW Doniphan, Ripley Co. (MCZ).

St. Francis River System

Little St. Francis River Drainage. *Missouri:* Little St. Francis River, 9 mi. E Ironton, Madison Co. (MZUM).

Meramec River System

Big River Drainage. *Missouri:* Mineral Fork, Washington Co. (Buchanan, 1977, fig. 48).

Meramec River Drainage. *Missouri:* Meramec River, Meramec State Park, Franklin Co. (MCZ).

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truncatus Spengler, *Unio* 96
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tuberculatus Barnes, *Unio* 90
tuberosa (Lea), *Quadrula* 87
tuberosus Lea, *Unio* 87
tumescens (Lea), *Fusconaia barnesiana* 87
turgidula (Lea), *Plagiola* 87, 97
undata (Barnes), *Fusconaia* 89
undatus Barnes, *Unio* 86
undulata (Say), *Alasmidonta* 99
undulatus (Say), *Strophitus* 93, 99, 107
utterbacki Frierson, *Pleurobema* 111
Utterbackia F. C. Baker 113
Utterbackiana Frierson 113
utterbackiana Frierson, *Quadrula tuberculata* 90
vanuxemensis (Lea), *Villosa* 87
vanuxemensis (Lea), *Villosa vanuxemensis* 113
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varicosa (Lamarck), *Alasmidonta* 99
ventricosa (Barnes), *Lampsilis* 95
ventricosus Barnes, *Unio* 95
venusta Gregorio, *Anodonta* 113
Venustaconcha Frierson 120
venustus Lea, *Unio* 94, 120
verrucosa (Rafinesque), *Tritogonia* 90
vibex (Conrad), *Villosa* 98, 113
Villosa Frierson 130
villosus Wright, *Unio* 130
virens Lea, *Anodonta* 92
virescens (Lea), *Lampsilis* 87, 88
virescens (Lea), *Unio* 88, 128

viridis Rafinesque, *Anodonta* 92
wagneri Baker, *Fusconaia undata* 89
wahlamatensis Lea, *Anodonta* 99
wardii Lea, *Unio* 90
wheeleri Ortmann and Walker, *Arkansia* 97, **119**
winnebagoensis Baker, *Lampsilis ventricosa* 95
winnebagoensis Baker, *Strophitus rugosus* 93

Plate 1.

The drainages of North America relevant to the post-glacial distribution of Unionacea.

Maximum Nebraskan glaciation is regarded as extending, roughly, to the present Missouri and Ohio rivers.

Wisconsin glaciation is marked by a double dotted line (After Flint, 1971, Fig. 21.1). No attention is paid to the several driftless areas since they do not have any bearing on unionid distribution.

The regions, systems, and drainages are marked by white letters in black circles.

A. Ozarkian Region. Consists of the Osage, Gasconade, and Meramec river systems above the Ozark Crest, and below it the St. Francis, White, Arkansas, Black and Red river systems. The latter two are not included on this map, but they appear on the distributional maps.
B. Cumberlandian Region
C. Mississippian Region
D. Ohioan Region
E. Northern Atlantic Slope Region
F. St. Lawrence River System (partial)

CANADIAN INTERIOR BASIN Insert from Clarke 1973, inside of front cover in some copies.

G. Pacific Coastal Region
H. Arctic Drainage
I. Hudson Bay Drainage
J. St. Lawrence River system (continued)

Areas of former confluences are marked by letters in white circles.

A. Area of confluence between the Minnesota and Red rivers.
B. Confluence of the Fox and Wisconsin rivers in the vicinity of Portage, Columbia Co., Wisconsin. Dotted lines in Lake Michigan indicate the now submerged Mackinac River system of which the Millecoquin River, in the eastern part of the Upper Michigan Peninsula, and the Carp and Ocqueoc, in the northern part of the Lower Peninsula, were once part.
C. Area of confluence of the Des Plaines River which, by way of the Chicago outlet, drained into the Illinois River. Before the formation of Lake Michigan, the Muskegon, Grand, and St. Joseph rivers of western Michigan connected with the Des Plaines River. The Muskegon River was tributary to the Grand, and these had a confluence with the Saginaw River.
D. Confluence of the Wabash and Maumee rivers in the vicinity of Fort Wayne, Allen Co., Indiana. During the Trent Stage, the Maumee flowed through the partially dry bed of Lake Erie into the Wabash. Many of the rivers presently flowing into Lake Erie were once part of the Greater Maumee drainage. Among these are the Clinton River which flows into Lake St. Clair; the Huron and Raisin rivers in eastern Michigan; the Sandusky, Vermilion, lower Cuyahoga, and Grand Rivers in Ohio; as well as the Grand River in Ontario. The Rouge River between the Clinton and Huron rivers was of later origin and was never connected to the Greater Maumee drainage.
E. Area of confluence of Lake Newberry, which inundated the Finger Lakes Basin and flowed south into the Susquehanna River.
F. Area of confluence between the Finger Lakes Basin and the Mohawk River.

Principal rivers and features mentioned in the tables and text which are not clearly visible on the map:

1. Ozark Crest
2. Black Water River
3. Meramec River
4. Monongahela River
5. Allegheny River
6. Tradewater River
7. Salt River
8. Ottawa River

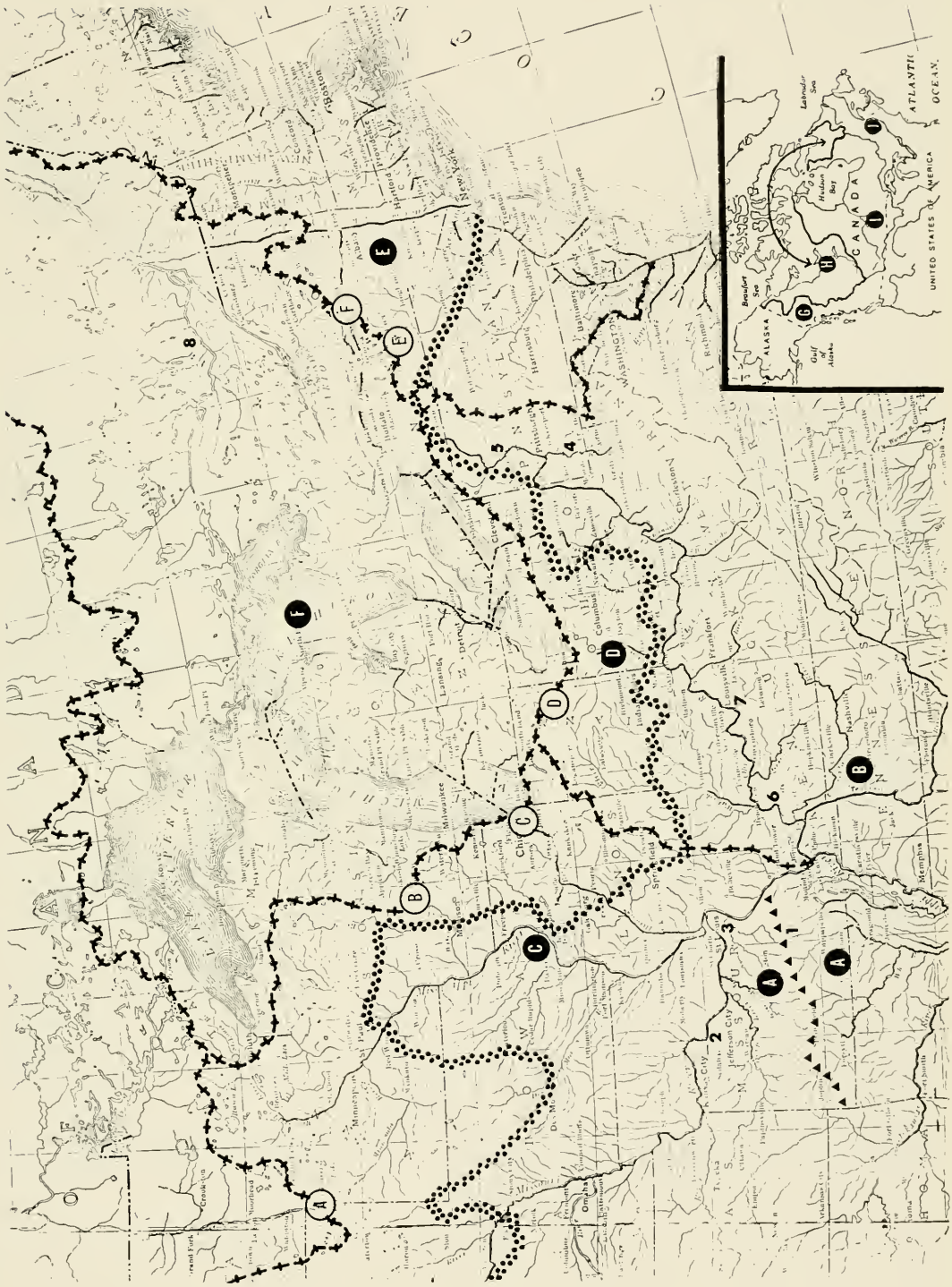

A
B
C
D
E
F
G
H
I
1
2
3
4
5
6
7
8
Labrador Sea
Hudson Bay
CANADA
ATLANTIC OCEAN
UNITED STATES OF AMERICA
Beaufort Sea
ALASKA
Gulf of Alaska
Minneapolis
Omaha
Memphis
Jefferson City
Springfield
Columbia
Frankfort
Nashville
Charleston
Harrisburg
Albany
New York
Boston
Milwaukee
Lansing
Columbus
Indianapolis
Chicago
Kansas City
Oklahoma City
Fort Worth
Austin
Dallas
Houston
Denver
Cheyenne
Bismarck
Pierre
Lincoln
Topeka
Jackson
Montgomery
Tallahassee
Atlanta
Raleigh
Richmond
Washington
Trenton
Harrisburg
Albany
Hartford
Providence
Augusta
Concord
Montpelier
Augusta
Portland
Salem
Olympia
Seattle
Spokane
Boise
Helena
Billings
Cheyenne
Santa Fe
Phoenix
Tucson
Los Angeles
San Diego
San Francisco
Sacramento
Reno
Carson City
Salt Lake City
Cheyenne
Denver
Pierre
Bismarck
Minneapolis
Madison
Lansing
Columbus
Indianapolis
Springfield
Jefferson City
Topeka
Lincoln
Omaha
Des Moines
Kansas City
Oklahoma City
Fort Worth
Austin
Dallas
Houston
Jackson
Montgomery
Tallahassee
Atlanta
Raleigh
Richmond
Washington
Trenton
Harrisburg
Albany
Hartford
Providence
Augusta
Concord
Montpelier
Augusta
Portland
Salem
Olympia
Seattle
Spokane
Boise
Helena
Billings
Cheyenne
Santa Fe
Phoenix
Tucson
Los Angeles
San Diego
San Francisco
Sacramento
Reno
Carson City
Salt Lake City

Plate 2.

The distribution of *Lampsilis abrupta* (Say) (squares), and *Lampsilis higginsi* (Lea) (dots). Triangles represent localities from which both species have been reported.

The distribution of these two closely related species suggests that *L. abrupta* had well established Pleistocene refugia in the Tennessee and Cumberland rivers, and probably also in the Monongahela and Allegheny rivers. It is the only Cumberlandian species to be found in the Mississippian region. While the Ozarkian species *L. higginsi* is found on both sides of the Ozark Crest, it is probable that the Meramec River drainage population was the Pleistocene refugium of the present Mississippian and Ohioan populations.

It appears that *L. abrupta* reached eastern Lake Erie during the Trent Stage, when the Maumee River flowed through the partially dry bed of Lake Erie into the Wabash as did *Proptera capax*, Plate 3.

Minneapolis
St. Paul
Winona
La Crosse
Dubuque
Waterloo
Cedar Rapids
Des Moines
Council Bluffs
Omaha
Sioux City
Missouri
Chicago
Milwaukee
Kenosha
Racine
Rockford
Aurora
Joliet
Kankakee
Ottawa
Peoria
Galesburg
Rock Island
Moline
Davenport
Muscatine
Burlington
Fort Madison
Keokuk
Hannibal
Quincy
Monroe
Louisiana
Alton
St. Louis
Jefferson City
Kansas City
St. Joseph
Atchison
Lawrence
Topeka
Ottawa
Emporia
Detroit
Lansing
Jackson
Kalamazoo
Battle Creek
Grand Rapids
Saginaw
Bay City
Port Huron
Toledo
Cleveland
Lorain
Sandusky
Akron
Canton
Pittsburgh
Beaver
Erie
Buffalo
Niagara Falls
Columbus
Springfield
Zanesville
Athens
Cincinnati
Hamilton
Middletown
Dayton
Portsmouth
Indianapolis
Richmond
Terre Haute
Logansport
Fort Wayne
Muncie
Lafayette
Evansville
New Albany
Jeffersonville
Louisville
Frankfort
Lexington
Owensboro
Bowling Green
Hopkinsville
Clarksville
Nashville
Murfreesboro
Chattanooga
Knoxville
Bristol
Kingsport
Johnson City
Asheville
Morganton
Hickory
Statesville
Salisbury
Concord
Charlotte
Gastonia
Spartanburg
Greenville
Greenwood
Anderson
Clemson
Seneca
Walhalla
Columbia
Orangeburg
Charleston
Georgetown
Florence
Darlington
Sumter
Wilmington
Fayetteville
Roanoke
Lynchburg
Danville
Martinsville
Winston Salem
Greensboro
High Point
Durham
Raleigh
Goldsboro
New Bern
Kinston
Rocky Mount
Tarboro
Greenville
Washington
Norfolk
Portsmouth
Petersburg
Richmond
Fredericksburg
Alexandria
Washington
Baltimore
Wheeling
Parkersburg
Huntington
Ashland
Ironton
Portsmouth
Charleston
Beckley
Bluefield
Princeton
Williamson
Pikeville
Hazard
Whitesburg
Harlan
Middlesboro
Cumberland Gap
Corbin
London
Somerset
Danville
Lebanon
Springfield
Columbia
Tullahoma
Shelbyville
Murfreesboro
Manchester
Cookeville
Crossville
Oneida
Huntsville
Decatur
Florence
Tuscumbia
Sheffield
Muscle Shoals
Gadsden
Anniston
Talladega
Birmingham
Bessemer
Tuscaloosa
Selma
Montgomery
Tuskegee
Auburn
Opelika
Columbus
West Point
Starkville
Columbus
Aberdeen
Tupelo
Corinth
Iuka
Memphis
Jackson
Vicksburg
Natchez
Tunica
Clarksdale
Greenville
Yazoo City
Meridian
Laurel
Hattiesburg
Gulfport
Biloxi
Pascagoula
Mobile
Pensacola
Tallahassee
Thomasville
Valdosta
Albany
Macon
Milledgeville
Augusta
Atlanta
Marietta
Griffin
Newnan
La Grange
Carrollton
Rome
Dalton
Chattanooga
Cleveland
Athens
Gainesville
Toccoa
Greenville
Spartanburg
Union
Rock Hill
Chester
Camden
Sumter
Florence
Dillon
Marion
Conway
Georgetown
Myrtle Beach
Wilmington
Jacksonville
Gainesville
Ocala
Orlando
Tampa
St. Petersburg
Sarasota
Bradenton
Fort Myers
Naples
Miami
Key West
Palm Beach
West Palm Beach
Fort Pierce
Vero Beach
Daytona Beach
Deland
Sanford
Kissimmee
Lakeland
Winter Haven
Bartow
Arcadia
Punta Gorda
Fort Meade
Plant City
Brooksville
Inverness
Crystal River
Cedar Key
Perry
Tallahassee
Quincy
Chipley
Marianna
Dothan
Eufaula
Abbeville
Greenville
Andalusia
Opp
Troy
Enterprise
Ozark
Fort Rucker
Brewton
Flomaton
Atmore
Bay Minette
Foley
Gulf Shores
Fairhope
Daphne
Spanish Fort
Robertsdale
Loxley
Elberta
Orange Beach
Perdido Beach
Pensacola
Milton
Crestview
Fort Walton Beach
Destin
Panama City
Port St. Joe
Apalachicola
Carrabelle
Wewahitchka
Blountstown
Bristol
Chattahoochee
Quincy
Havana
Monticello
Madison
Live Oak
Lake City
Jasper
White Springs
Jennings
Fernandina Beach
St. Augustine
Palatka
Crescent City
Interlachen
Starke
Macclenny
Baldwin
Callahan
Hilliard
Yulee
Kingsland
St. Marys
Folkston
Waycross
Douglas
Alma
Hazlehurst
Baxley
Jesup
Brunswick
Darien
Thomasville
Moultrie
Tifton
Cordele
Fitzgerald
Ashburn
Sylvester
Albany
Americus
Dawson
Bainbridge
Cairo
Thomasville
Quitman
Valdosta
Nashville
Ocilla
Fitzgerald
Douglas
Waycross
Folkston
Kingsland
St. Marys
Brunswick
Darien
Jesup
Baxley
Hazlehurst
Alma

Plate 3.

The distribution of *Proptera capax* (Green). This species appears to have had Pleistocene refugia in the Ozarkian Region, but only below the Ozark Crest. It is presumed that *capax* reached eastern Lake Erie, and at least one tributary of western Lake Ontario, during the Trent Stage, when the Maumee River flowed through the partially dry bed of Lake Erie into the Wabash.

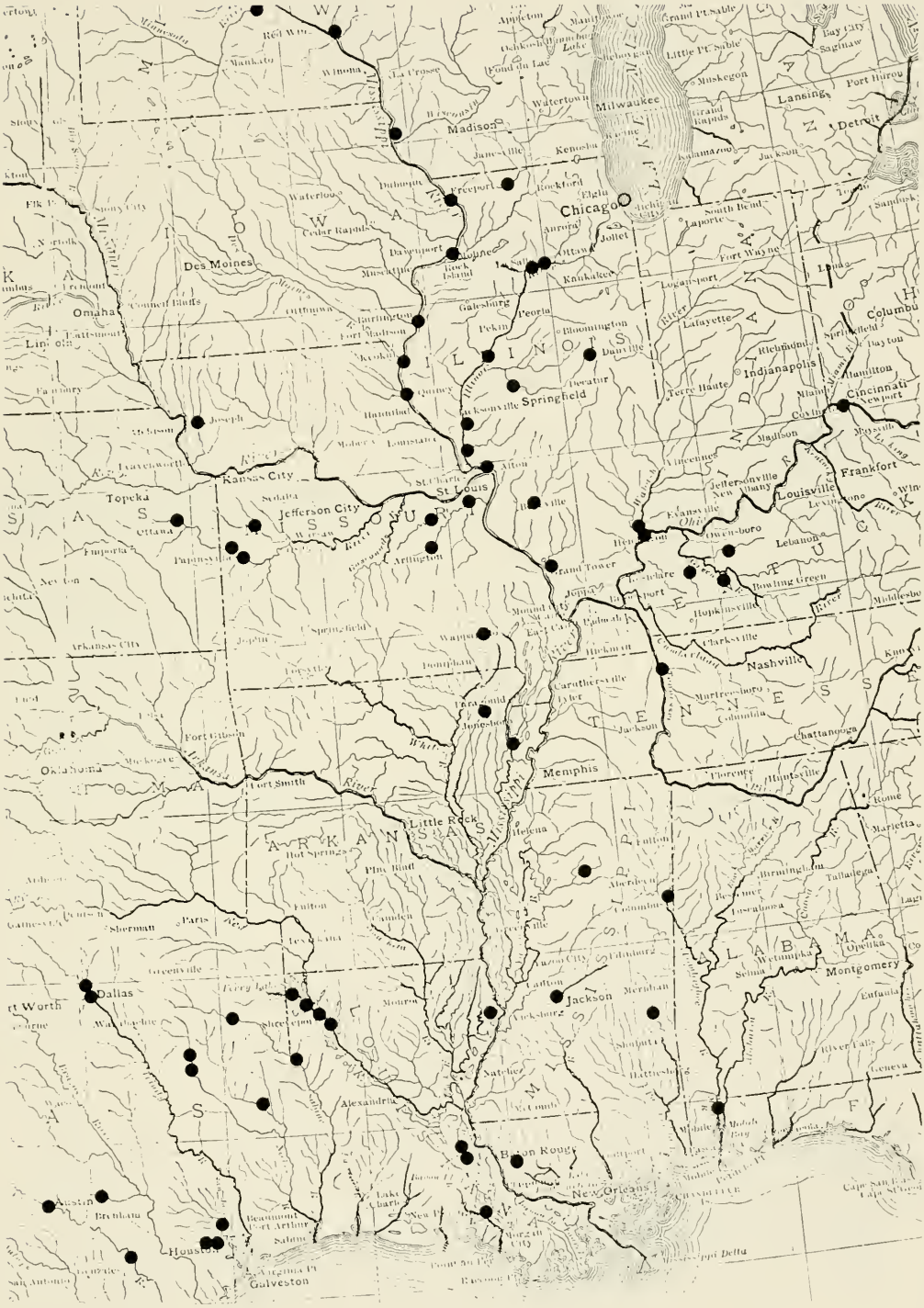
Minneapolis
St. Paul
Stillwater
Eau Claire
WISCONSIN
Red Wing
Mankato
Winona
La Crosse
Wisconsin River
Fond du Lac
Oshkosh
Appleton
Green Bay
Manistee
Grand Pt. Sable
Bay City
Saginaw
Niagara Falls
Buffalo
Milwaukee
Racine
Little Pt. Sable
Muskegon
Lansing
Fort Huron
Madison
Janesville
Kenosha
Kalamazoo
Jackson
Detroit
Erie
Cleveland
Waterloo
Dubuque
Freeport
Rockford
Elgin
Chicago
Aurora
Joliet
South Bend
Laporte
Sandusky
Lorain
Youngstown
Canton
Pittsburg
Des Moines
Cedar Rapids
Davenport
Rock Island
Muscatine
Ottumwa
Burlington
Fort Madison
Galesburg
Peoria
Kankakee
Fort Wayne
Mansfield
Steubenville
Wheeling
Keokuk
Quincy
Hannibal
Jacksonville
Springfield
Decatur
Bloomington
Danville
Lafayette
Logansport
Delaware
Columbus
Newark
Zanesville
Lancaster
Parkersburg
Clarksburg
Grafton
Fairmont
Richmond
Indianapolis
Terre Haute
Hamilton
Cincinnati
Newport
Portsmouth
Ironton
Charleston
St. Joseph
Moberly
Louisiana
Kansas City
Sedalia
St Charles
St Louis
Alton
Vincennes
Madison
Jeffersonville
New Albany
Frankfort
Louisville
Lexington
Winchester
Jefferson City
Warsaw
Belleville
Evansville
Owensboro
Lebanon
Arlington
Grand Tower
Rosiclare
Cairo
Bowling Green
Hopkinsville
Bristol
Winston-Salem
Joplin
Springfield
Wappapello
Paducah
Mound City
Hickman
Clarksville
Nashville
Knoxville
Salisbury
Concord
Charlotte
Ga-tonia
Dyersburg
Carutherville
Tyler
Murfreesboro
Columbia
Jonesboro
Jackson
Chattanooga
Spartanburg
Greenville
Fort Gibson
Fort Smith
Memphis
Florence
Huntsville
Gainesville
Columbia
Rome
Marietta
Atlanta
Athens
Augusta
Little Rock
Hot Springs
Pine Bluff
Helena
Fulton
Aberdeen
Birmingham
Talladega
Grima
Milledgeville
Fulton
Camden
Columbus
Bessemer
Tuscaloosa
Lagrange
Macon
ARKANSAS
MISSOURI
ILLINOIS
INDIANA
OHIO
KENTUCKY
TENNESSEE
WEST VIRG
NORTH
SOUTH
CAROLINA
GEORGIA
LAKE MICHIGAN
LAKE ERIE

Plate 4.

The distribution of *Arcidens confragosus* (Say). The unconfirmed record from the St. Lawrence River System: Great Lakes Drainage (Lake Michigan). *Illinois:* Chicago, Cook Co. is represented by an open circle. Records from the James River Drainage, South Dakota, of the Missouri River System, are beyond the limits of the map.

This species is widely distributed in the Gulf Coastal Region and in tributaries of the Mississippi south of the Ozark Crest. It is possible that the Meramac River drainage was the Pleistocene refugium of the present Mississippian and Ohioan populations. It is assumed that the one record from the Tennessee River is the result of the recent introduction of fishes behind Kentucky Dam. If this is so, in all probability this species reached the Ohioan Region from the west in post-glacial time, though it may have had a refugium in the Green River Drainage.

It is not impossible that *A. confragosus* reached Lake Michigan when the rivers of western Michigan, i.e. the Grand, the Muskegon, and the Saginaw, connected with the Des Plaines River, through the Chicago outlet and Illinois River to the Mississippi. Nevertheless, this record could not be confirmed and since it has never been reported elsewhere in Lake Michigan, and since the open lake in the vicinity of Chicago does not appear to be a propitious environment for it, this record is regarded as spurious.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Red Wing
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La Crosse
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Milwaukee
Chicago
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Cedar Rapids
Dubuque
Davenport
Rock Island
Freeport
Rockford
Des Moines
Council Bluffs
Omaha
Galesburg
Peoria
Bloomington
Springfield
Quincy
Hannibal
Joseph
Kansas City
St. Louis
Topeka
Jefferson City
Arlington
Grand Tower
Cairo
Memphis
Little Rock
Hot Springs
Fort Smith
Oklahoma
Dallas
Fort Worth
Sherman
Paris
Texarkana
Shreveport
Alexandria
Natchez
Vicksburg
Jackson
Meridian
Baton Rouge
New Orleans
Houston
Galveston
Austin
Beaumont
Port Arthur
Lake Charles
Detroit
Lansing
Grand Rapids
Kalamazoo
Fort Wayne
South Bend
Indianapolis
Terre Haute
Cincinnati
Louisville
Frankfort
Owensboro
Evansville
Nashville
Chattanooga
Knoxville
Birmingham
Montgomery
Mobile
Pensacola
Tallahassee
Atlanta
Columbus
Dayton
Springfield
Hamilton
Lafayette
Logansport
Jeffersonville
Lebanon
Bowling Green
Hopkinsville
Clarksville
Martinsburg
Columbia
Florence
Huntsville
Rome
Marietta
Talladega
Selma
Eufaula
Troy
Opelika
Wetumpka
Montgomery
Evergreen
Greenville
Monroe
Natchitoches
Alexandria
Hattiesburg
Meridian
Jackson
Vicksburg
Natchez
Baton Rouge
New Orleans
Lake Charles
Beaumont
Port Arthur
Houston
Galveston
Austin
Brenham
Waco
Abilene
Fulton
Pine Bluff
Hot Springs
Arkansas City
Joplin
Springfield
Topeka
Ottawa
Emporia
Atchison
Leavenworth
Lincoln
Omaha
Council Bluffs
Des Moines
Waterloo
Cedar Rapids
Dubuque
Davenport
Rock Island
Freeport
Rockford
Elgin
Chicago
Aurora
Joliet
Ottawa
Kankakee
Galesburg
Peoria
Bloomington
Springfield
Quincy
Hannibal
Joseph
Kansas City
St. Louis
Alton

Plate 5.

The distribution of *Anodonta suborbiculata* Say. Records from the Big Blue and Elkhorn river drainages, Nebraska, of the Missouri River System, are beyond the limits of the map.

The distribution of this species in the Gulf Coastal Region is discontinuous, as it is in the tributaries of the Mississippi, south of the Ozark Crest. It is impossible to isolate a single refugium for the present Mississippian and Ohioan populations. It is assumed that the one record from the Tennessee River is the result of the recent introduction of fishes behind Wheeler Dam. If this is so, then in all probability this species reached the Ohioan Region from the west in postglacial time, though it may have had a refugium in the Green River drainage.

Anodonta suborbiculata, like *A. corpulenta*, *Villosa lienosa*, *Ligumia subrostrata*, and *Uniomerus tetralasmus*, is a species which does not usually inhabit large rivers, but is more often found in smaller streams, sloughs or lakes.

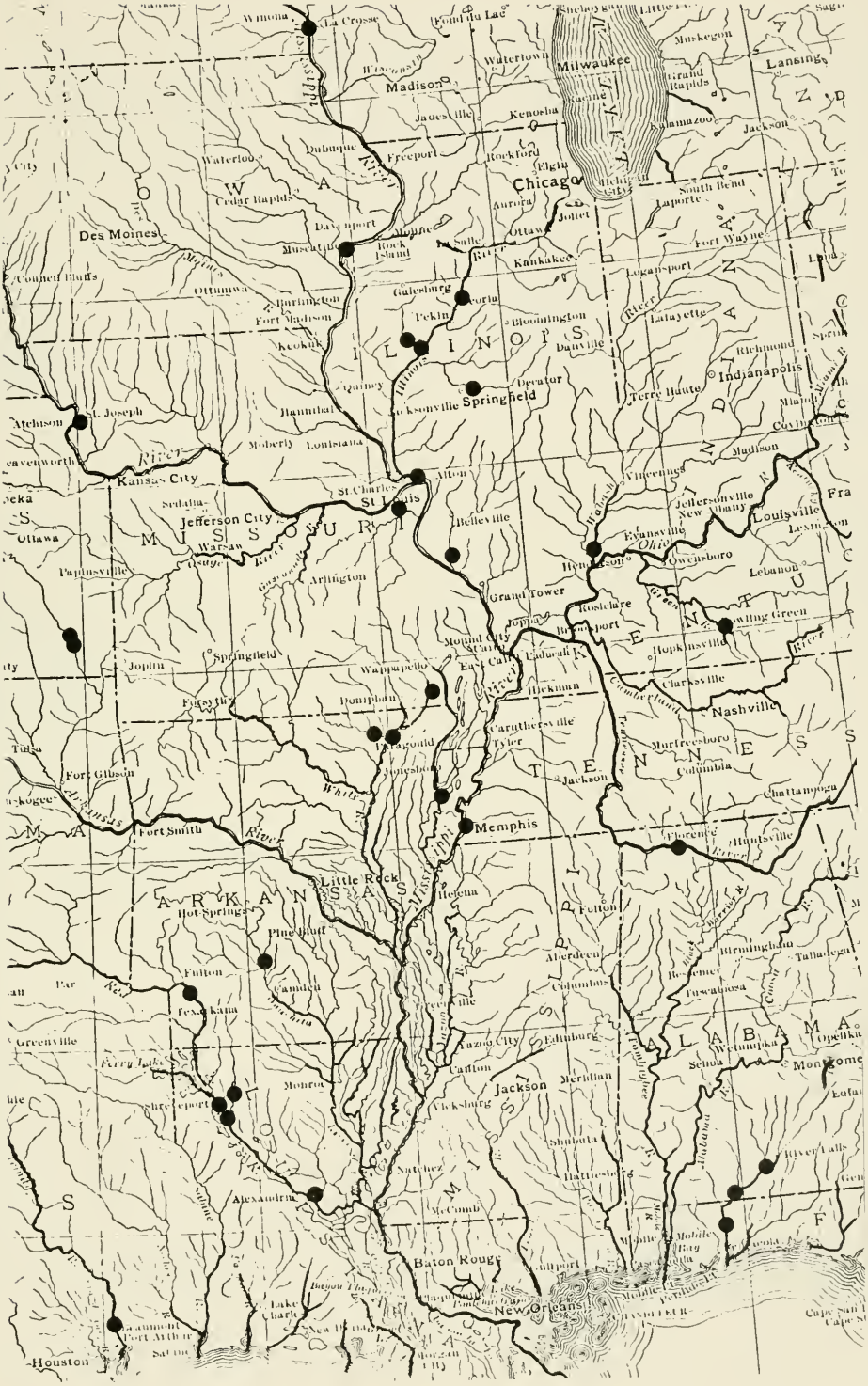
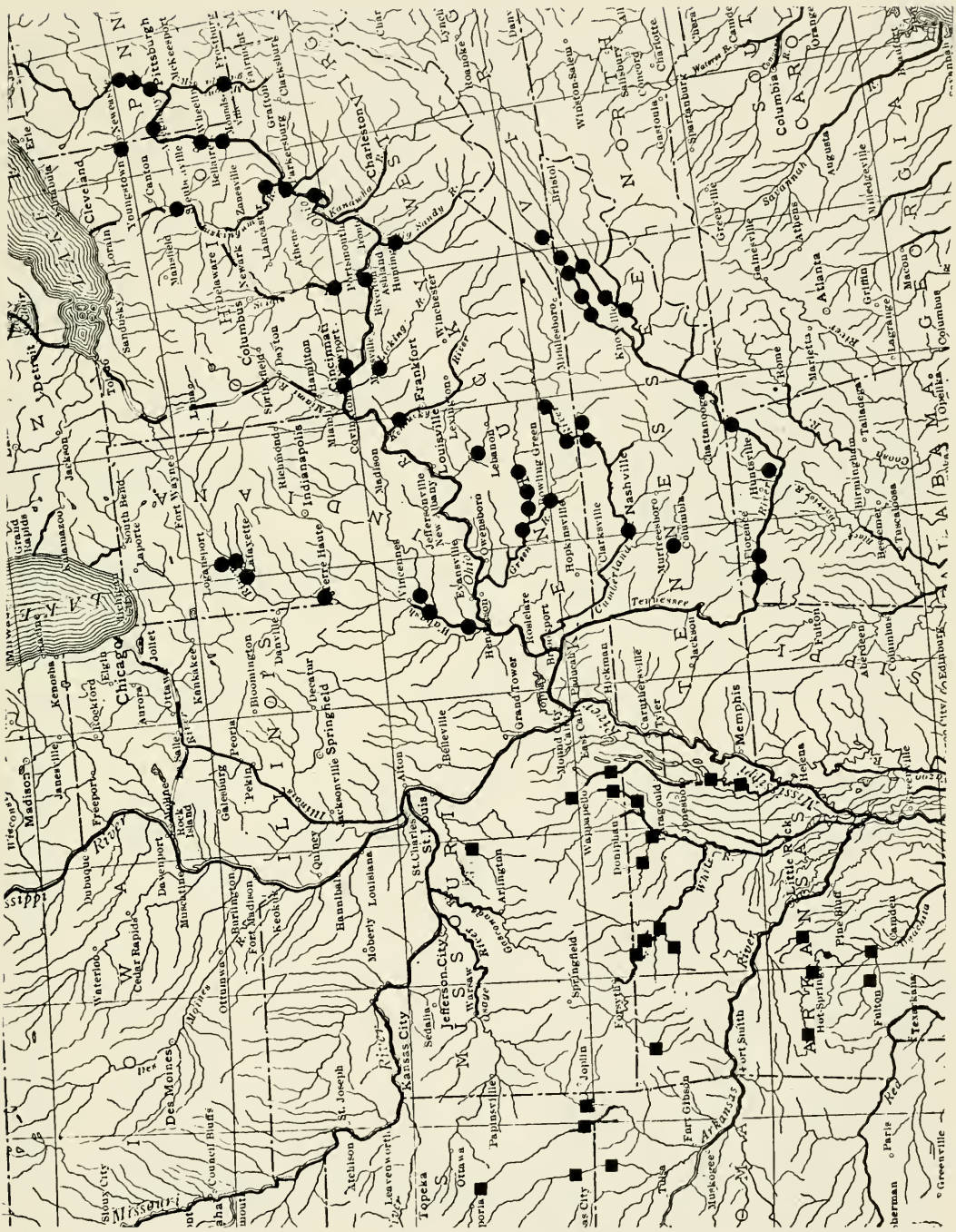

Winona
La Crosse
Fond du Lac
Milwaukee
Muskegon
Lansing
Madison
Watertown
Grand Rapids
Jacksonville
Kenosha
Kalamazoo
Jackson
Dubuque
Freeport
Rockford
Elgin
Chicago
South Bend
Waterloo
Cedar Rapids
Aurora
Joliet
Davenport
Rock Island
Ottawa
Fort Wayne
Des Moines
Muscatine
La Salle
Kankakee
Council Bluffs
Ottumwa
Burlington
Galesburg
Peoria
Logansport
Fort Madison
Keokuk
Pekin
Bloomington
Lafayette
Quincy
Decatur
Springfield
Terre Haute
Indianapolis
Richmond
St. Joseph
Hannibal
Atchison
Moberly
Louisiana
Madison
Leavenworth
Kansas City
St Charles
Alton
St Louis
Vincennes
Jefferson City
Belleville
Jeffersonville
New Albany
Louisville
Ottawa
Warsaw
Evansville
Owensboro
Lebanon
Paphsville
Arlington
Grand Tower
Rockport
Bowling Green
Springfield
Joplin
Mound City
Cairo
Paducah
Hopkinsville
Wappapello
Hickman
Clarksville
Poplar Bluff
Dunklin
Carrutherville
Nashville
Tyler
Murfreesboro
Columbia
Jackson
Fort Gibson
Memphis
Chattanooga
Fort Smith
Florence
Huntsville
Little Rock
Hot Springs
Helena
Fulton
Pine Bluff
Aberdeen
Birmingham
Talladega
Columbus
Tuscaloosa
Fulton
Texarkana
Camden
Greenville
Vicksburg
Jackson
Meridian
Monroe
Shreveport
Natchez
Alexandria
Mobile
Baton Rouge
Pensacola
New Orleans
Lake Charles
Houston
Beaumont
Port Arthur

Plate 6.

The distribution of *Cyprogenia aberti* (Conrad) (squares) and *Cyprogenia stegaria* (Rafinesque) (dots).

Cyprogenia aberti (Conrad) is found only in the Ozarkian Region. Below the Ozark Crest it is widely distributed; above the Crest, it is restricted to the Meramec River system.

Cyprogenia stegaria (Rafinesque). This species has persisted in the Cumberlandian Region, and may have had additional refugia in the Green, Allegheny and Monongahela river drainages.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Cleveland
Pittsburgh
Detroit
Columbus
Cincinnati
Indianapolis
Louisville
Nashville
Memphis
Atlanta
Birmingham
Knoxville
Chattanooga
Charleston
Wheeling
Frankfort
Evansville
Springfield
Dayton
Toledo
Akron
Canton
Youngstown
Erie
Buffalo
Rochester
Syracuse
Albany
Utica
Scranton
Harrisburg
Philadelphia
Baltimore
Washington
Richmond
Norfolk
Roanoke
Lynchburg
Charlottesville
Fredericksburg
Petersburg
Wilmington
Raleigh
Greensboro
Winston-Salem
Charlotte
Asheville
Columbia
Greenville
Spartanburg
Augusta
Savannah
Macon
Columbus
Montgomery
Mobile
Pensacola
Tallahassee
Jacksonville
Tampa
Orlando
Miami
Key West
Gainesville
Ocala
Daytona Beach
St. Augustine
Fort Myers
Sarasota
Bradenton
Lakeland
Tallahassee
Dothan
Selma
Tuscaloosa
Florence
Huntsville
Decatur
Gadsden
Anniston
Rome
Dalton
Cleveland
Chattanooga
Kingsport
Johnson City
Bristol
Abingdon
Pulaski
Radford
Roanoke
Lynchburg
Danville
Martinsville
Winston-Salem
Greensboro
High Point
Asheboro
Fayetteville
Wilmington
Jacksonville
Goldsboro
New Bern
Kinston
Rocky Mount
Greenville
Tarboro
Elizabeth City
Norfolk
Virginia Beach
Newport News
Hampton
Williamsburg
Richmond
Petersburg
Hopewell
Colonial Heights
Fredericksburg
Alexandria
Arlington
Falls Church
Manassas
Culpeper
Warrenton
Leesburg
Winchester
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Plate 7.

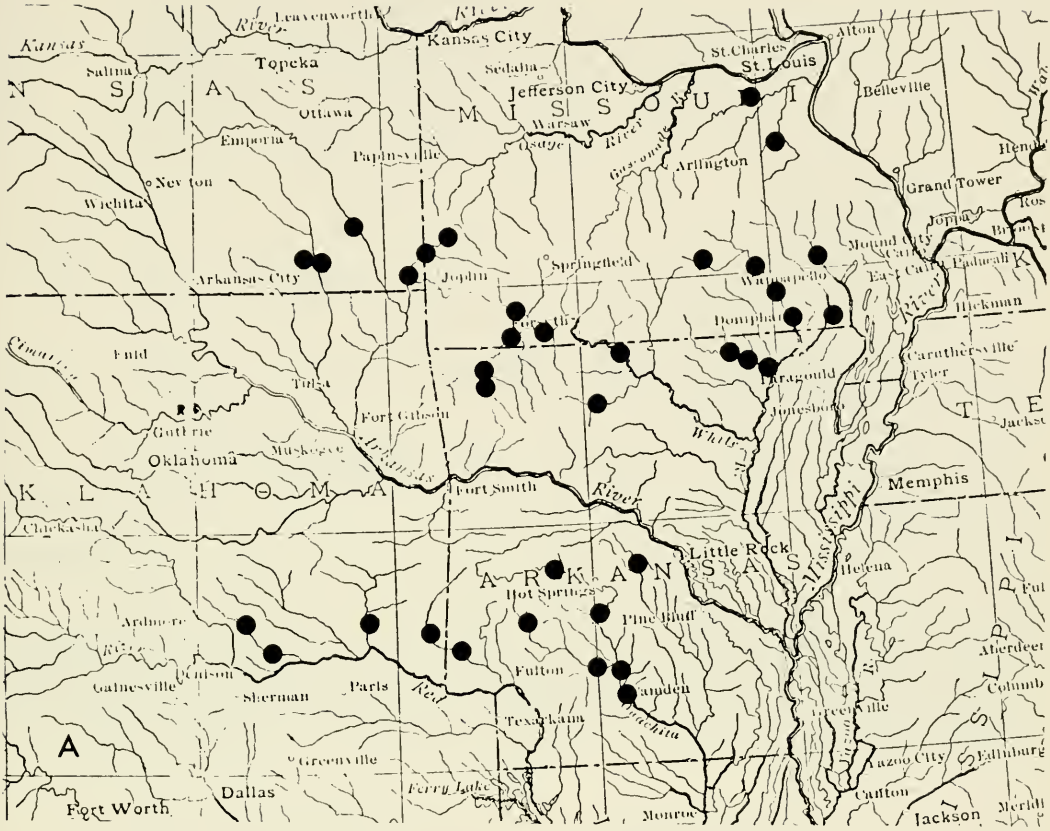
A. The distribution of *Ptychobranchus occidentalis* (Conrad).

Found only in the Ozarkian Region, below the Ozark Crest from the Red to the St. Francis river systems; above the Crest, it is restricted to the Meramec River system.

Ptychobranchus fasciolare (Rafinesque) (Table 2 C, Table 3 A), a closely related species, that has persisted in the Cumberlandian Region, and may have had additional refugia in the Green, Allegheny and Monongahela river drainages, has a distribution in the Ohioan region, which is very similar to *Cyprogenia stegaria* (Rafinesque) (Plate 6, dots). In addition, it spread into Lake Erie (Plate 1 D).

B. The distribution of *Villosa reeviana* (Lea).

Found only in the Ozarkian Region, below the Ozark Crest in the White River system; above the Crest, it occurs in the Osage, Gasconade, and Meramec river systems.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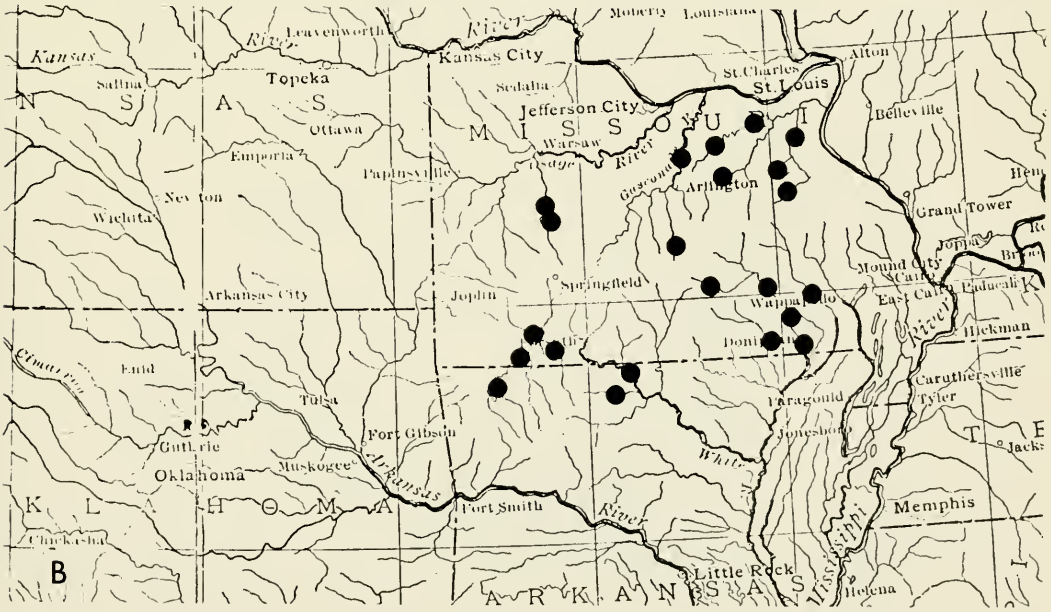
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Plate 8.

A. The distribution of *Fusconaia ozarkensis* (Call) (dots), *Arkansia wheeleri* Ortmann and Walker (triangles), and *Villosa arkansasensis* (Lea) (squares).

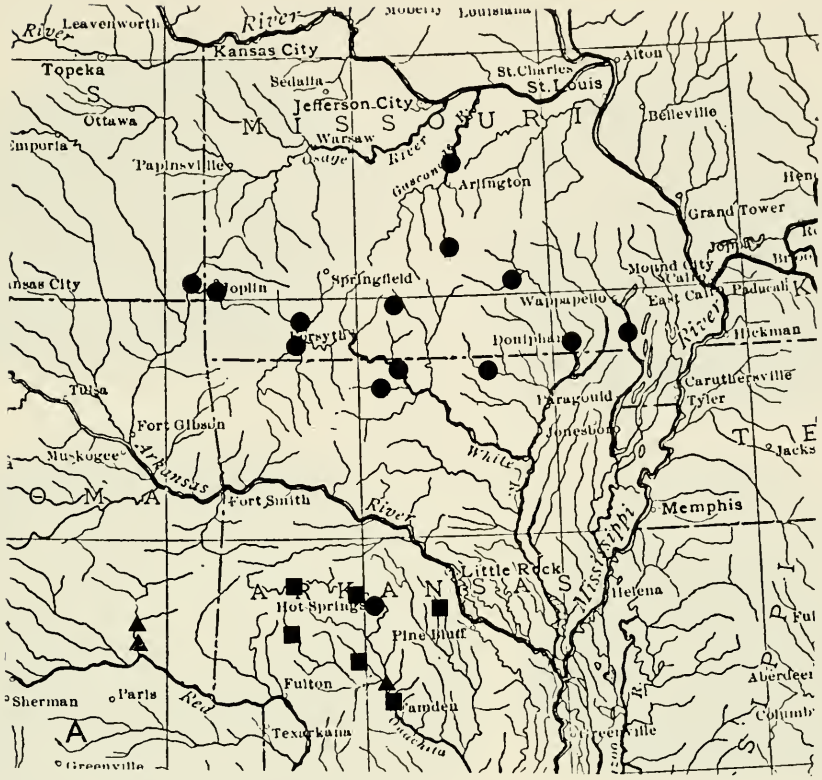
Fusconaia ozarkensis (Call) is found only in the Ozarkian Region, below the Ozark Crest, in the Ouachita River drainage of the Black River system, the Neosho River drainage of the Arkansas River system, the White and St. Francis river systems; above the Crest it is restricted to the Gasconade River system.

Arkansia wheeleri Ortmann and Walker is found only in the Ozarkian Region, below the Ozark Crest, in the upper Red and Black river systems.

Villosa arkansasensis (Lea) is found only in the Ozarkian Region, below the Ozark Crest, in the upper Black River system.

B. The distribution of *Actinonaias rafinesqueana* (Frierson) (dots), and *Lampsilis powelli* (Lea) (triangles).

Actinonaias rafinesqueana (Frierson) is found only in the Ozarkian Region below the Ozark Crest, in the upper Red and White river systems. The location of the Black River record is conjecture. This species is close to the Cumberlandian species, *Actinonaias pectorosa* (Conrad). *Lampsilis powelli* (Lea) is found only in the Ozarkian Region, below the Ozark Crest, in the Saline River drainage of the Black River system; the upper Arkansas, and upper White river systems. The location of the White River record is conjecture. This species is close to the Cumberlandian species, *Lampsilis virescens* (Lea).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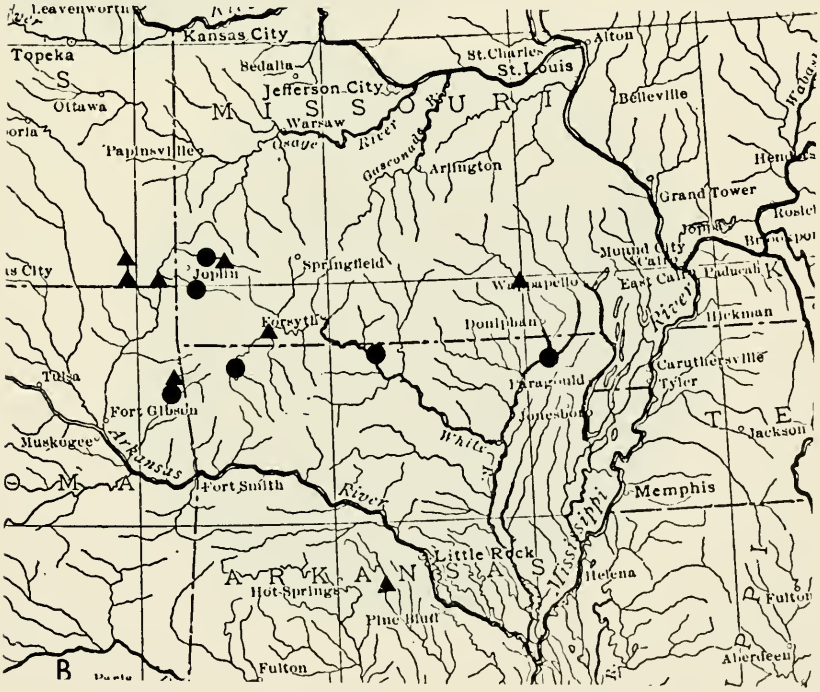
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White River
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Jackson
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Plate 9.

Fusconaia ozarkensis (Call)

Figure 1. *Unio ozarkensis* Call. Big Creek, [of Current River], Texas Co., Missouri. Paralectotype MCZ 5710. Length 55, height 37, width 19 mm.

Figure 2. *Pleurobema brevis subelliptica* Simpson. Spring River, Hardy, Fulton Co., Arkansas. Paralectotype USNM 159952a. Length 43, height 28, width 16 mm.

Figure 3. *Pleurobema utterbackii* Frierson. White River, Hollister, Taney Co., Missouri. Holotype MCZ 271448, right valve. Length 68, height 42, width 26 mm.

Figure 4. *Quadrula flava sampsoniana* Frierson. Elk River, McDonald Co., Missouri. Holotype MZUM 92226. Length 54, height 37, width 19 mm.

Anodonta (*Utterbackia*) *suborbiculata* Say

Figure 5. Mercer Bayou, N Black Diamond, Miller Co., Arkansas. MCZ 293508. Length 71, height 58, width 26 mm.

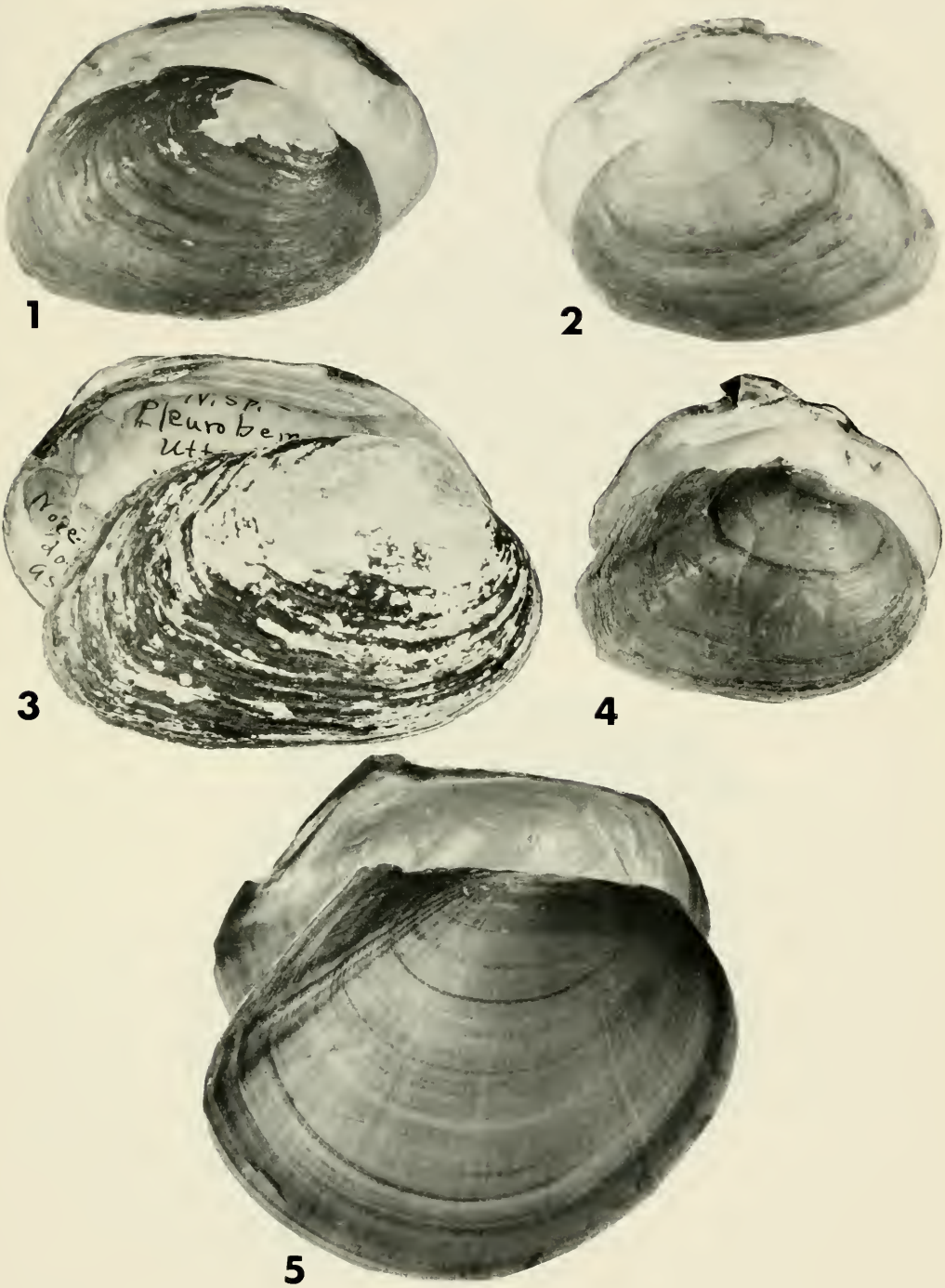
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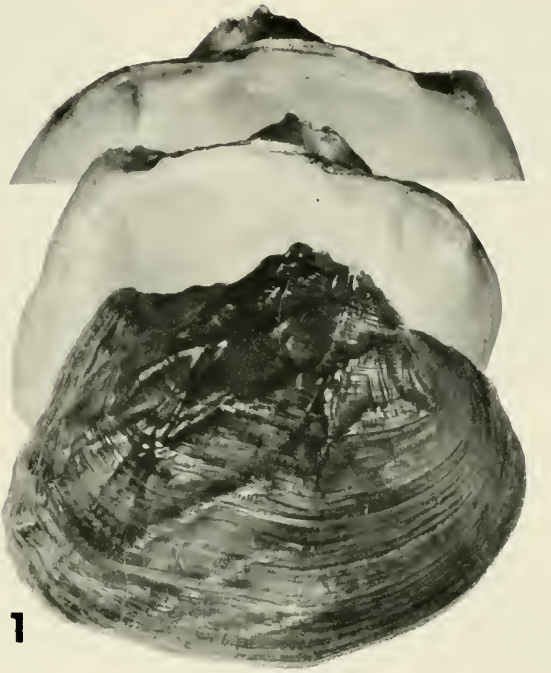
Plate 10.

Arcidens confragosus (Say)

Figure 1. *Alasmidonta confragosa* Say. Fox River of the [Little] Wabash [River, Richland Co., Illinois]. Topotype MCZ 53004. Length 88, height 68, width 45 mm.

Figure 2. *Arcidens confragosa jacintoensis* Strecker. San Jacinto River, Liberty Co., Texas. Topotype MCZ 23317. Length 82, height 57, width 32 mm.



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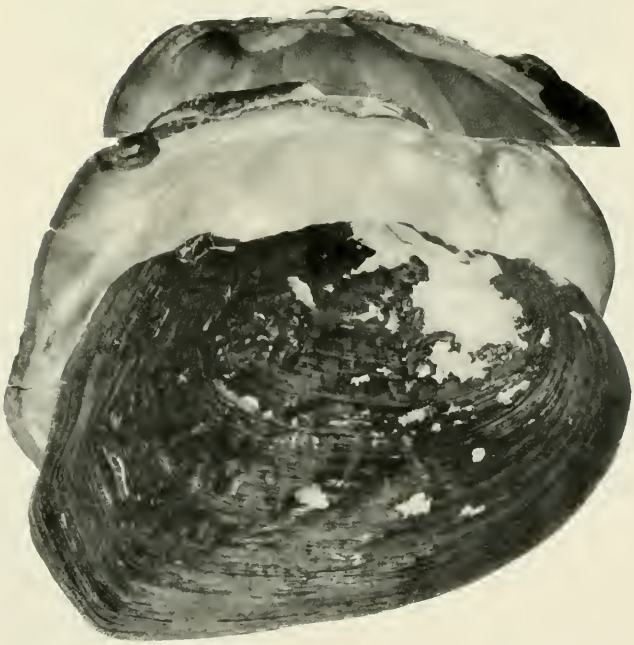

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Plate 11.

Arkansia wheeleri Ortmann and Walker

Figure 1. *Arkansia wheeleri* Ortmann and Walker. Old River [a bayou of the Ouachita River], Arkadelphia, Clark Co., Arkansas. Holotype MZUM 105514. Length 73.5, height 62, width 41 mm.

Actinonaias rafinesqueana (Frierson)

Figure 2. *Lampsilis rafinesqueana* Frierson. Illinois River, Moodys, Cherokee Co., Oklahoma. Holotype MZUM 87576. Length 86, height 60, width 35 mm. Female.

Figure 3. *Lampsilis rafinesqueana* Frierson. Illinois River, Moodys, Cherokee Co., Oklahoma. Paratype MZUM 90665. Length 69, height 43, width 26 mm. Female.

Figure 4. *Lampsilis rafinesqueana* Frierson. Illinois River, Moodys, Cherokee Co., Oklahoma. Paratype MZUM 90665. Length 62, height 37, width 21 mm. Male.

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Plate 12.

Lampsilis (*Lampsilis*) *abrupta* (Say)

Figure 1. Ohio River, Cincinnati, Hamilton Co., Ohio. MCZ 37526. Length 82, height 63, width 40 mm. Male.

Figure 2. *Unio abruptus* Say. Wabash [River, New Harmony, Posey Co., Indiana]. Figured holotype [lost] from Say. Length 71, height 60, width 40 mm [based on original figure]. Female.

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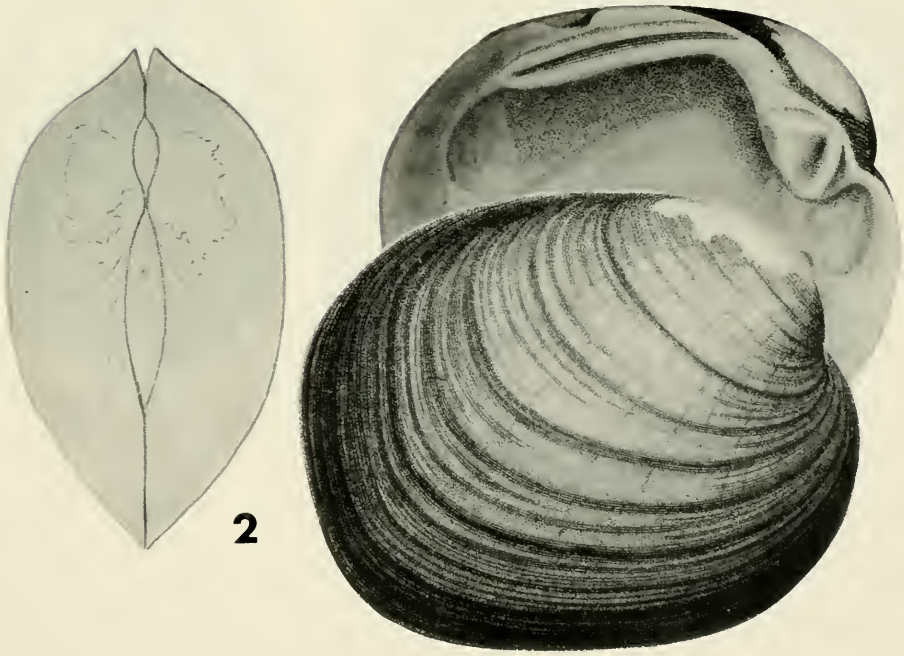

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Plate 13.

Lampsilis (*Lampsilis*) *higginsi* (Lea)

Figure 1. *Unio higginsii* Lea. [Mississippi River], Muscatine, [Muscatine Co.], Iowa. Holotype USNM 84823. Length 81, height 59, width 48 mm. Male.

Figure 2. Mississippi River, near Aledo, Mercer Co., Illinois. MCZ 288383. Length 81, height 61, width 51 mm. Female.

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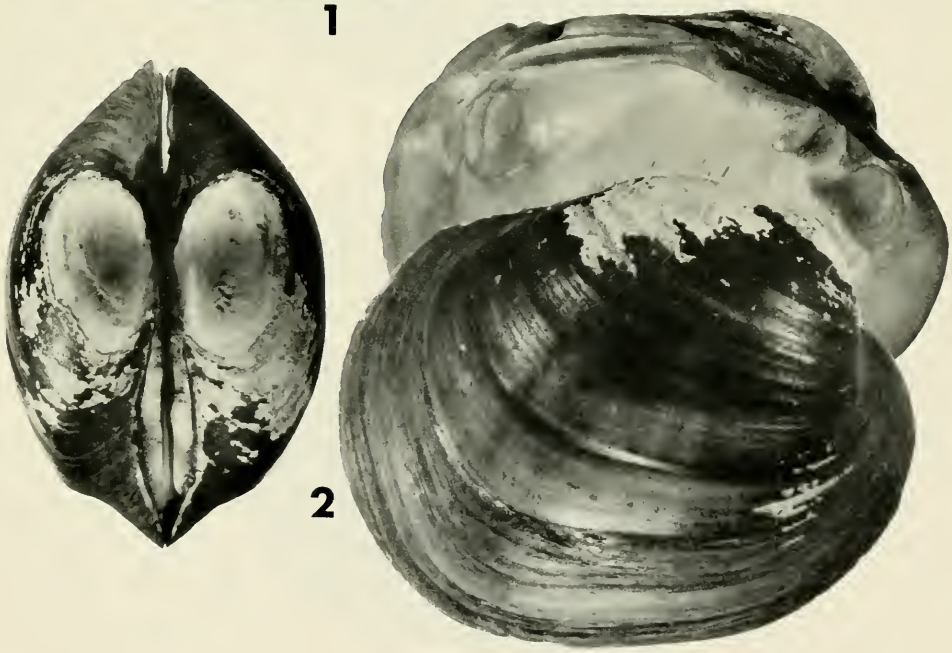

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Plate 14.

Lampsilis satur (Lea)

Figure 1. *Unio satur* Lea [Red River], Alexandria, [Rapides Parish], Louisiana. Holotype USNM 84505. Length 80, height 61, width 51 mm. Female.

Figure 2. Saline River, Benton, Saline Co., Arkansas. MZUM 33758. Length 74, height 55, width 35 mm. Male.

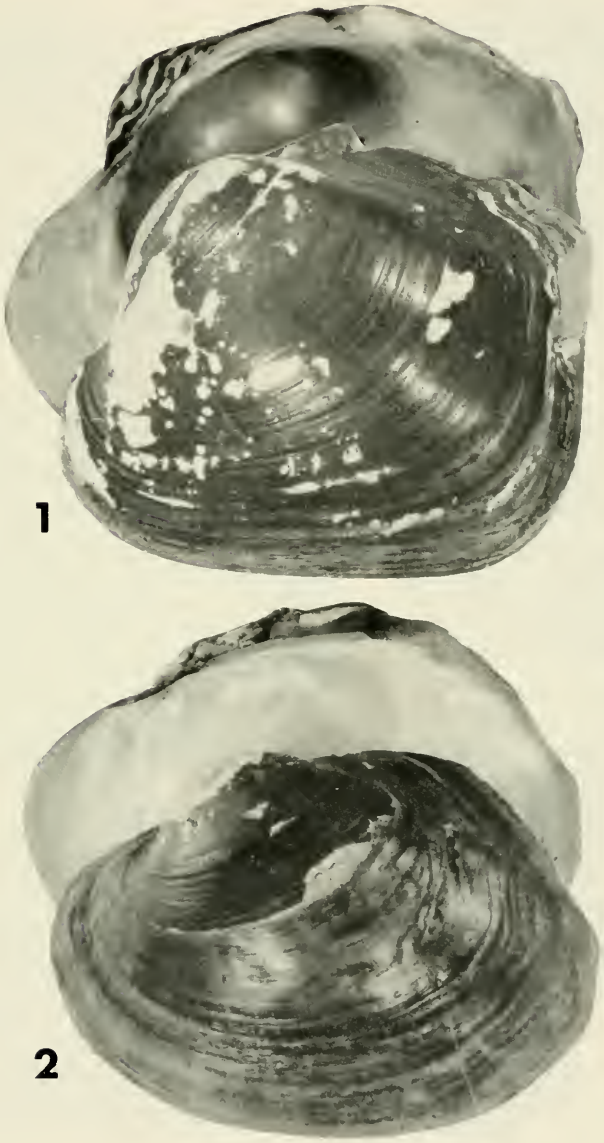
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Plate 15.

Lampsilis excavata (Lea)

Figure 1. Saline River, Benton, Saline Co., Arkansas. MCZ 293585. Length 72, height 50, width 33. Male.

Figure 2. Saline River, Benton, Saline Co., Arkansas. MCZ 293585. Length 78, height 54, width 38 mm. Female.

Lampsilis powelli (Lea)

Figure 3. *Unio powelli* Lea. Saline River, Arkansas. Holotype USNM 85024. Length 80, height 56, width 29 mm. Male.

Figure 4. *Unio powelli* Lea. Saline River, Arkansas. Allotype USNM 85024a. Length 77, height 39, width 24 mm. Female.

Lampsilis hydiana (Lea)

Figure 5. *Unio hydianus* Lea. Teche River, [St. Landry Parish], Louisiana. Holotype USNM 85010. Length 64, height 37, width 27 mm. Male.

Figure 6. *Unio hydianus* Lea. [Red River], Alexandria [Rapides Parish], Louisiana. Allotype USNM 85010a. Length 57, height 37, width 28 mm. Female.

Figure 7. *Unio placitus* Lea. 1852. Alabama. Holotype USNM 85152. Length 34, height 22, width 15 mm. Male.

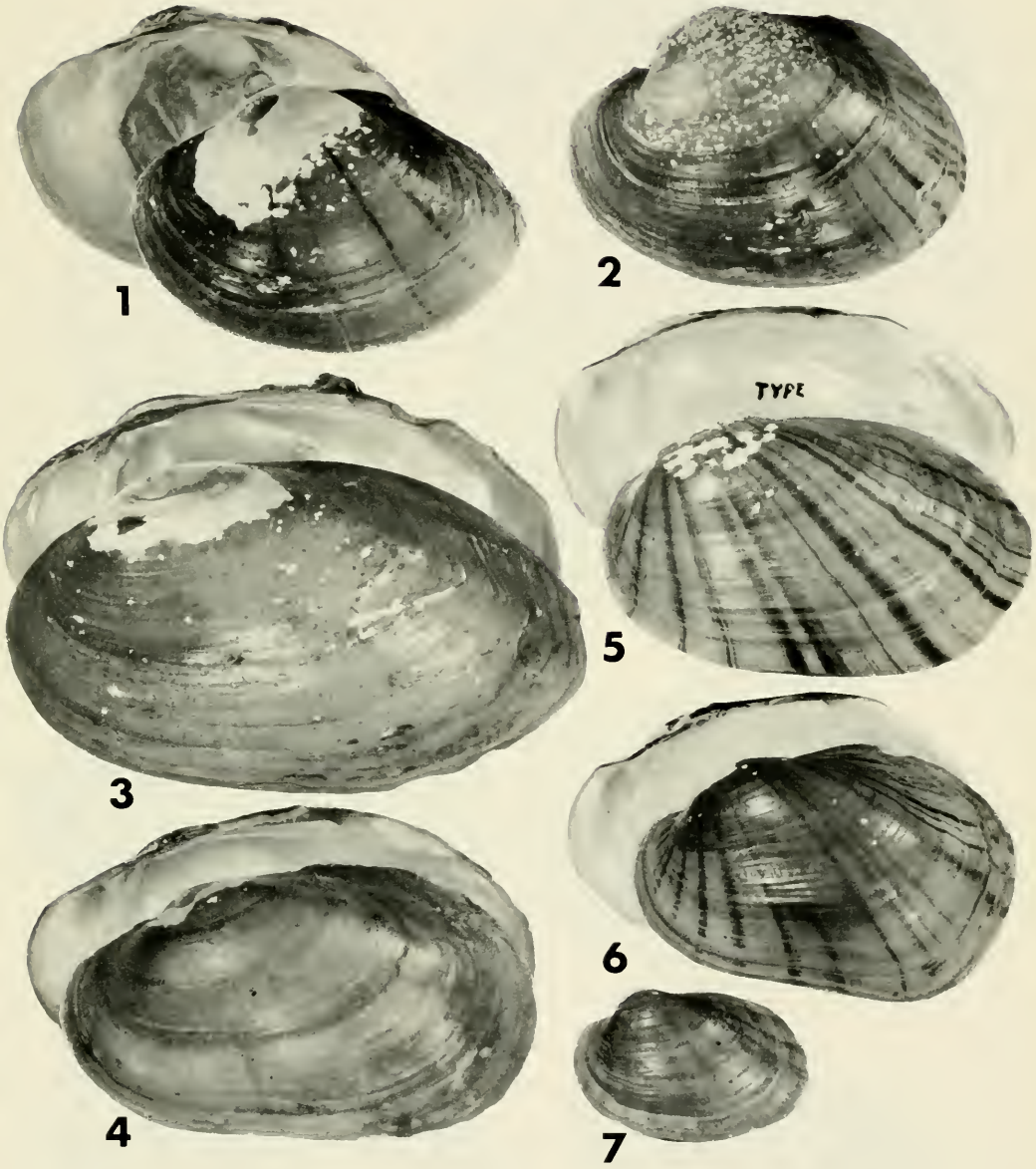
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Plate 16.

Proptera capax (Green)

Figure 1. Mississippi River, Muscatine, Muscatine Co., Iowa. MCZ 5043. Length 79, height 59, width 54 mm.

Figure 2. Niagara River, Buffalo, Erie Co., New York. Collected by Elizabeth Letson, 1906, with the note, "Only one I ever found." Buffalo Museum of Science (approx. nat. size).

Villosa arkansasensis (Lea)

Figure 3. *Unio arkansasensis* Lea. [Ouachita River] near Hot Springs, Garland Co., Arkansas. Holotype USNM 25710. Length 40, height 28, width 18 mm. Male.

Figure 4. Saline River, Benton, Saline Co., Arkansas. MCZ 4989. Length 37, height 27, width 18 mm. Female.

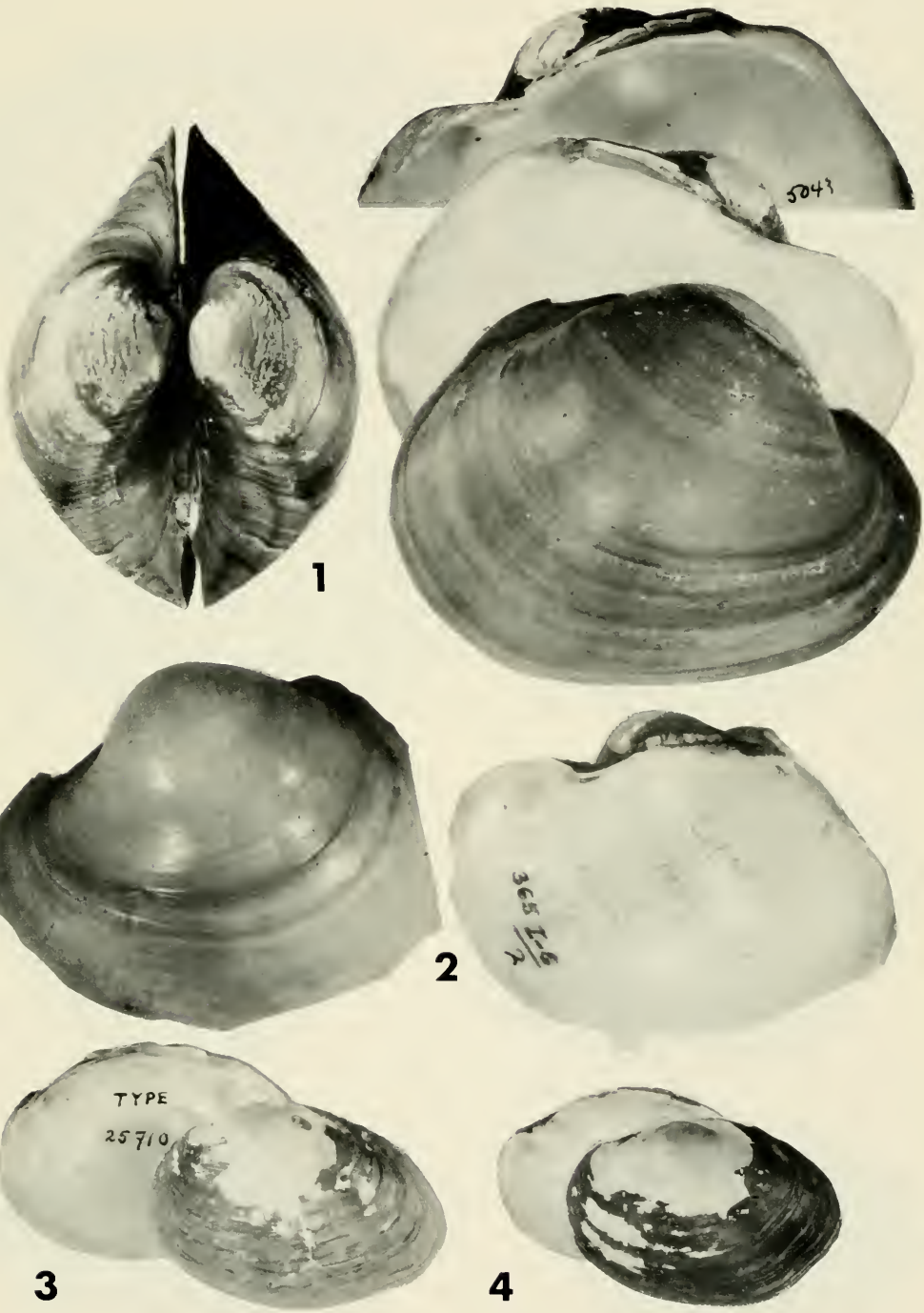
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Plate 17.

Villosa reeviana (Lea)

Figure 1. *Unio reevianus* Lea. [White River, Elkins, Washington Co., Arkansas]. Holotype USNM 85025. Length 75, height 41, width 28 mm. Male.

Figure 2. *Unio reevianus* Lea. White River, Arkansas. Allotype USNM 85025a. Length 62, height 40, width 24 mm. Female.

Figure 3. *Unio breviculus* Call. Jacks Fork [of Current River, Shannon Co.], Missouri. Lectotype MCZ 5020. Length 64, height 40, width 24 mm. Male.

Figure 4. *Unio breviculus* Call. Big Creek [of Current River, Texas Co.]Missouri. Allotype MCZ 5023. Length 58, height 40, width 25 mm. Female.

Figure 5. *Lampsilis brittsi* Simpson. [Little Niangua River, Camden Co., Missouri. Topotype MCZ 293574, from J. P. Britts. Length 47, height 30, width 18 mm. Female.

Villosa vibex (Conrad)

Figure 6. *Lampsilis streckeri* Frierson. Little Red River, Arkansas. Holotype MZUM 91075. Length 65, height 38, width 22 mm. Male.

Figure 7. Onion Creek [Colorado River system], Travis Co., Texas. MZUM 79921. Length 49, height 31, width 16 mm. Male.

Figure 8. Onion Creek [Colorado River System], Travis Co., Texas. MZUM 79921. Length 53, height 32, width 19 mm. Female.

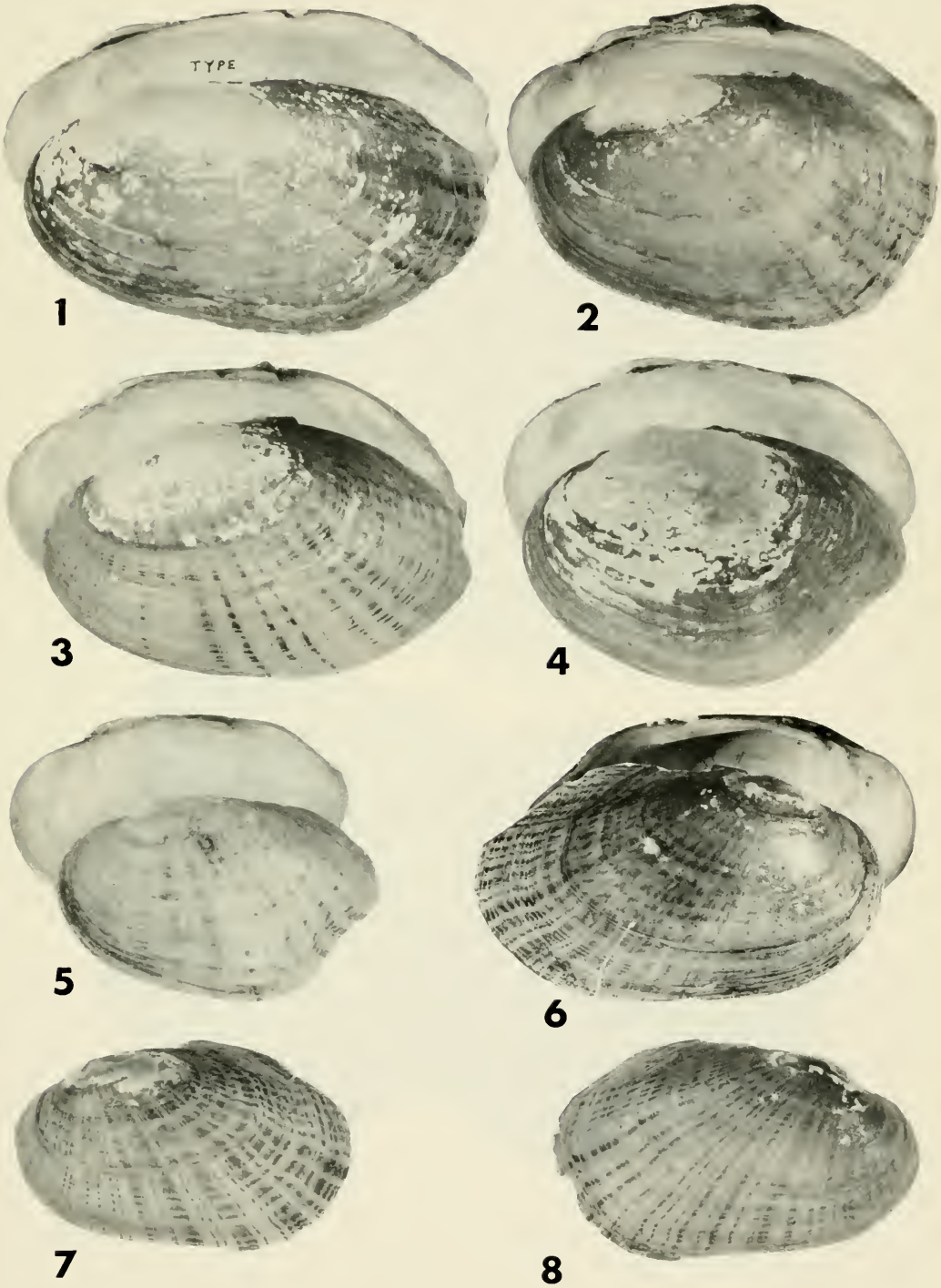
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Plate 18.

Cyprogenia stegaria (Rafinesque)

Figure 1. *Obovaria stegaria* Rafinesque. Ohio River. Lectotype ANSP 20215. Length 47, height 49, width 32 mm.

Figure 2. *Unio irroratus* Lea. Ohio River, Cincinnati, Hamilton Co., Ohio; T. G. Lea. Paratype USNM 84299; the figured holotype is missing. Length 51, height 54, width 35 mm.

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Plate 19.

Cyprogenia stegaria (Rafinesque)

Figure 1. *Cyprogenia irrorata pusilla* Simpson. Green River, Mammoth Cave, Edmonson Co., Kentucky. Lectotype USNM 152004. Length 43, height 37, width 29 mm.

Figure 2. Tuscarawas River, New Philadelphia, Tuscarawas Co., Ohio. MCZ 14409. Length 50, height 45, width 27 mm.

Cyprogenia aberti (Conrad)

Figure 3. Saint Francis River, Wittsburg, Cross Co., Arkansas. MCZ 5492. Length 48, height 46, width 29 mm.

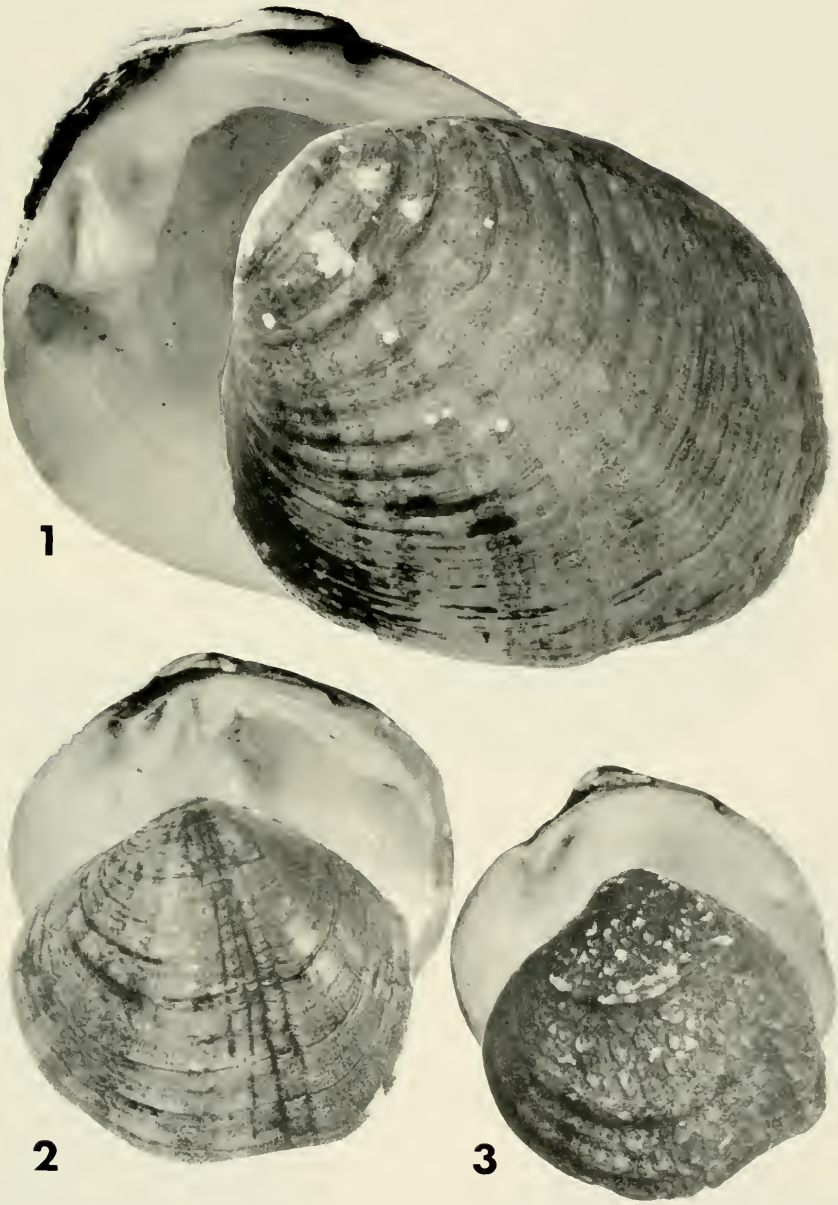
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Plate 20.

Cyprogenia aberti (Conrad)

Figure 1. *Unio aberti* Conrad. Rapids of Verdigris River, Chambers Ford [not located; Oklahoma]. Figured holotype [lost] after Conrad. Length 40, height 34, width 15 mm.

Figure 2. *Unio lamarckianus* Lea. White River, Arkansas. Holotype USNM 84306. Length 37, height 30.5, width 13 mm.

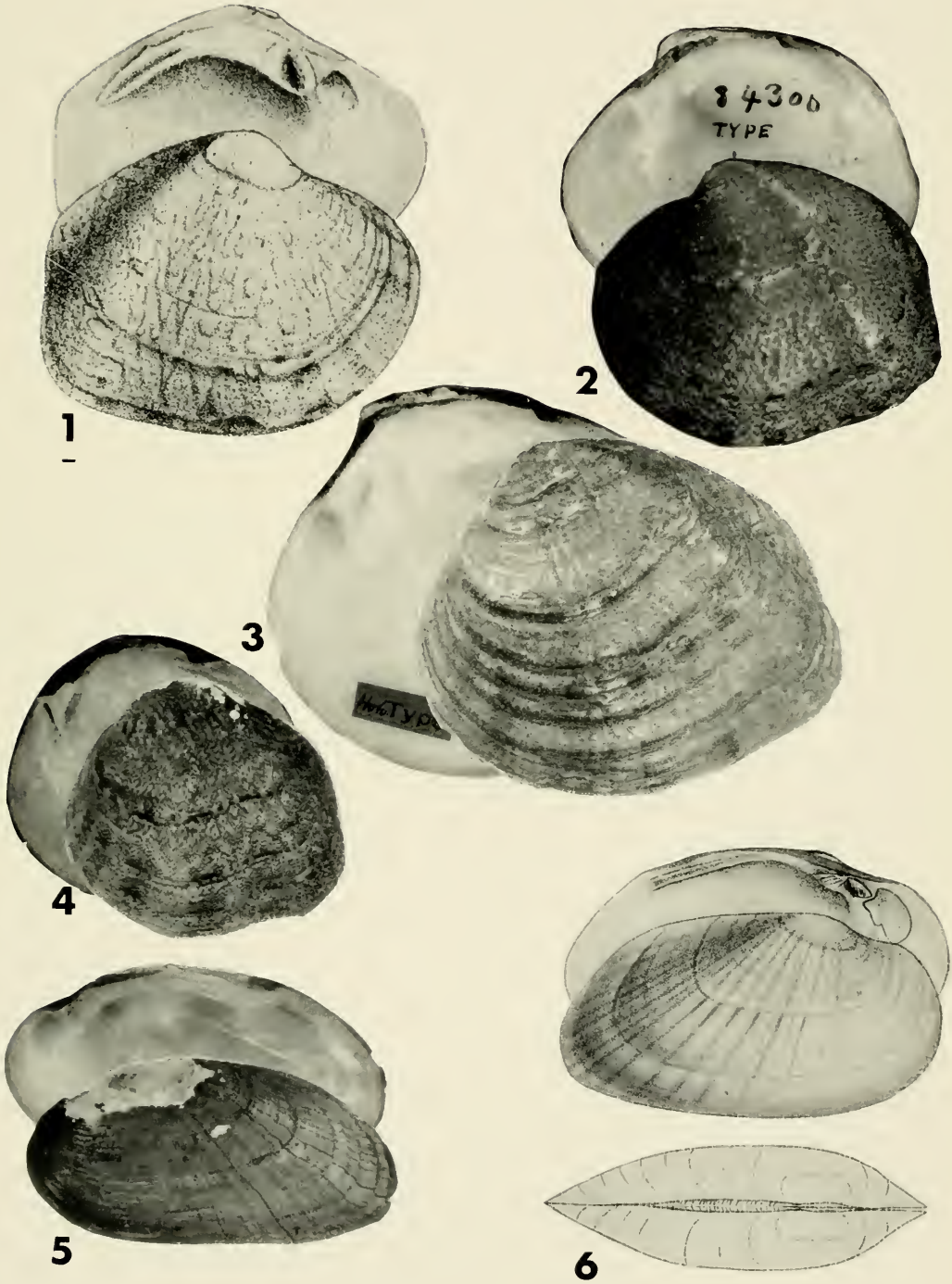
Figure 3. *Unio popenoi* Call. Fall River, Wilson Co., Kansas. Holotype MCZ 4943. Length 78, height 68, width 39 mm.

Figure 4. Meramec River, [near Franklin Co. line]. Crawford Co., Missouri. Specimen loaned by R. D. Oesch. Length 39, height 37, width 24 mm.

Ptychobranchus occidentalis (Conrad)

Figure 5. *Ptychobranchus clintonensis* Simpson. Archies Fork of Little Red River, near Clinton, Van Buren Co., Arkansas. Paratype MCZ 192371. Length 57, height 29, width 16 mm.

Figure 6. *Unio occidentalis* Conrad. Currant [Current] River, [Randolph Co.], Arkansas. Figured holotype [lost] from Conrad. Length 52, height 28, width 17 mm [based on original figure].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A Phyletic Study of the Lake Tanganyika Cichlid Genera *Asprotilapia, Ectodus, Lestradea, Cunningtonia, Ophthalmochromis,* and *Ophthalmotilapia*

KAREL F. LIEM

HARVARD UNIVERSITY
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A PHYLETIC STUDY OF THE LAKE TANGANYIKA CICHLID GENERA *ASPROTILAPIA, ECTODUS, LESTRADEA, CUNNINGTONIA, OPHTHALMOCHROMIS,* AND *OPHTHALMOTILAPIA*

KAREL F. LIEM[1]

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ABSTRACT. On the basis of comparative osteology and myology, *Asprotilapia, Ectodus, Lestradea, Cunningtonia, Ophthalmochromis,* and *Ophthalmotilapia* of Lake Tanganyika are hypothesized to be members of a monophyletic lineage of cichlid fishes. All members share the following suite of characters: (1) the entopterygoid is widely separated from the palatine; (2) the posterior and dorsal margins of the palatine form a 90° angle; (3) the slender hyomandibula has a long symplectic process and a very reduced hyomandibular flange; (4) the anterior margin of the pterosphenoid is notched; (5) the vertical depth of the metapterygoid is shallow; (6) the operculum has a distinct auricular process; (7) the transversus dorsalis muscle is reduced; and (8) the obliquus posterior muscle is enlarged. These characters are considered specialized when compared with the accepted generalized morphology of *Astatotilapia*. The phyletic relationships of this lineage are documented by synapomorphies that distinguish subunits of decreasing levels of universality within the assemblage. *Asprotilapia* represents a highly specialized branch with six major skeletomuscular specializations. The remaining five genera are pictured as a second lineage, of which *Ectodus* is the most generalized taxon. On the basis of recency of common descent, *Ophthalmochromis* is synonymized with the genus *Ophthalmotilapia*. Although there is no doubt that the *Ophthalmotilapia* lineage has undergone extensive morphological radiation in both skull structure and dentition, the data on morphology, function, trophic ecology, and behavior of this and other cichlid lineages have failed to establish unequivocally that the morphological radiation is also adaptive. The morphological and functional pattern in this lineage reinforces the paradox that morphologically and phylogenetically most specialized cichlid taxa are not only remarkable specialists but also jacks-of-all-trades.

INTRODUCTION

The precise phylogenetic interrelationships of the endemic cichlids in Lake Tanganyika are still unknown (e.g., Fryer and Iles, 1972: 507). Essentially the problem is to distinguish groups that are true, hierarchically evolved sister groups showing increasing specialization or apomorphy, from groups that are gradal assemblages of polyphyletic ancestry (Greenwood, 1974, 1979). Liem and Stewart (1976) have shown that the lepidophagous cichlids of Lake Tanganyika represent a monophyletic lineage. Recently Liem (1979) has postulated that because of the basic homogeneity in specialized morphology and function, the invertebrate picking cichlids of Lake Tanganyika must have originated from a common ancestor. Greenwood (1979) has synonymized *Limnotilapia* with *Simo-*

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chromis to show the close phyletic relationships of two genera previously pictured as belonging to two different lineages (Fryer and Iles, 1972: 507). A complete analysis of phyletic relationships for the endemic cichlids is hindered because of an apparent absence of synapomorphic features which would enable one to build up the various levels of relationship, and a phyletic analysis of cichlids from other lakes and rivers. This paper is part of a series dealing with the establishment of monophyletic lineages. Such an attempt represents a first step toward the ultimate goal of interrelating the different lineages on a sister group basis.

This paper deals with six endemic genera of Lake Tanganyika: *Asprotilapia*, Boulenger, 1901; *Ectodus*, Boulenger, 1900; *Lestradea*, Poll, 1943; *Cunningtonia*, Boulenger, 1906; *Ophthalmotilapia*, Boulenger, 1901; and *Ophthalmochromis*, Poll, 1956. Except for *Ectodus*, this assemblage is characterized as predominantly herbivorous, inhabiting rocky habitats of Lake Tanganyika down to a depth of 15 m. *Ectodus* is especially abundant in shallower and sandy habitats. With the exception of *Ectodus descampsi*, all members of the group possess long intestinal tracts (2.5–6 times the standard length) and exploit filamentous and unicellular algae, diatoms, crustaceans, and insect larvae as food sources. Based on comparative osteological and myological data, I am presenting a hypothesis that the assemblage is monophyletic, with *Asprotilapia* as a very specialized form, and *Ectodus* and *Lestradea* as the least specialized representatives.

In this study only a limited number of functional data have been gathered from *Lestradea* and *Ophthalmotilapia*. However, much information from other cichlids (Liem, 1978, 1979, 1980) can be applied to this lineage in determining the nature and possible evolutionary direction of the character complexes. A provisional phylogenetic scheme is presented as a hypothesis, with each branch defined by its unique morphological specializations.

MATERIALS AND METHODS

Osteological studies are based on alizarin preparations and some dried skeletons. Osteological nomenclature follows Liem and Stewart (1976) and Barel *et al.* (1976). The myology has been studied from formalin fixed specimens, which are stored in 70% ethyl alcohol. With very few exceptions the nomenclature of Winterbottom (1974) and Anker (1978) is followed. All drawings were made by means of the Wild-M5 camera lucida.

The following specimens from the British Museum (BM) and the Museum of Comparative Zoology (MCZ) have been studied:

Asprotilapia leptura BM 1906.9.6.157
Asprotilapia leptura BM 671 (dried skeleton)
Aulonocranus dewindti BM 1960.9.30.4642–4656
Aulonocranus dewindti MCZ 49305
Callochromis macrops BM 1960.9.30.2821–2823
Callochromis melanostigma BM 1960.9.30.2845–2859
Callochromis pleurospilus MCZ 49280
Cardiopharynx schoutedeni BM 1960.9.30.1574–1615
Cunningtonia longiventralis MCZ 49243
Cunningtonia longiventralis BM 1960.9.30.1912–1919
Ectodus descampsi BM 1961.11.22.113–119
Grammatotria lemairei MCZ 49277
Grammatotria lemairei BM 1960.9.30.3317–3330
Astatotilapia ("Haplochromis") burtoni BM 1960.9.30.2415–2433
Lamprologus elongatus BM 1960.9.30.6790–6793
Lamprologus elongatus MCZ 49251
Lamprologus moorei MCZ 49245
Leptochromis calliurus BM 1960.9.30.3351–3353
Lestradea perspicax perspicax BM 1960.9.30.1468–1484
Limnochromis auritus BM 1960.9.30.1981–1985
Ophthalmochromis nasutus MCZ 49232
Ophthalmochromis ventralis BM 1960.9.30.1689–1694
Ophthalmochromis ventralis MCZ 49232
Ophthalmotilapia boops BM 1960.9.30.1720–1724
Ophthalmotilapia boops BM 1960.9.30.1716–1718
Sarotherodon nilotica MCZ 49312
Trematocara unimaculatum BM 1961.11.22.519–528
Trematocara unimaculatum MCZ 49262
Tylochromis polylepis BM 1960.9.30.109–113
Xenotilapia ornatipinnis MCZ 49266
Xenotilapia sima BM 1961.11.22.208–211

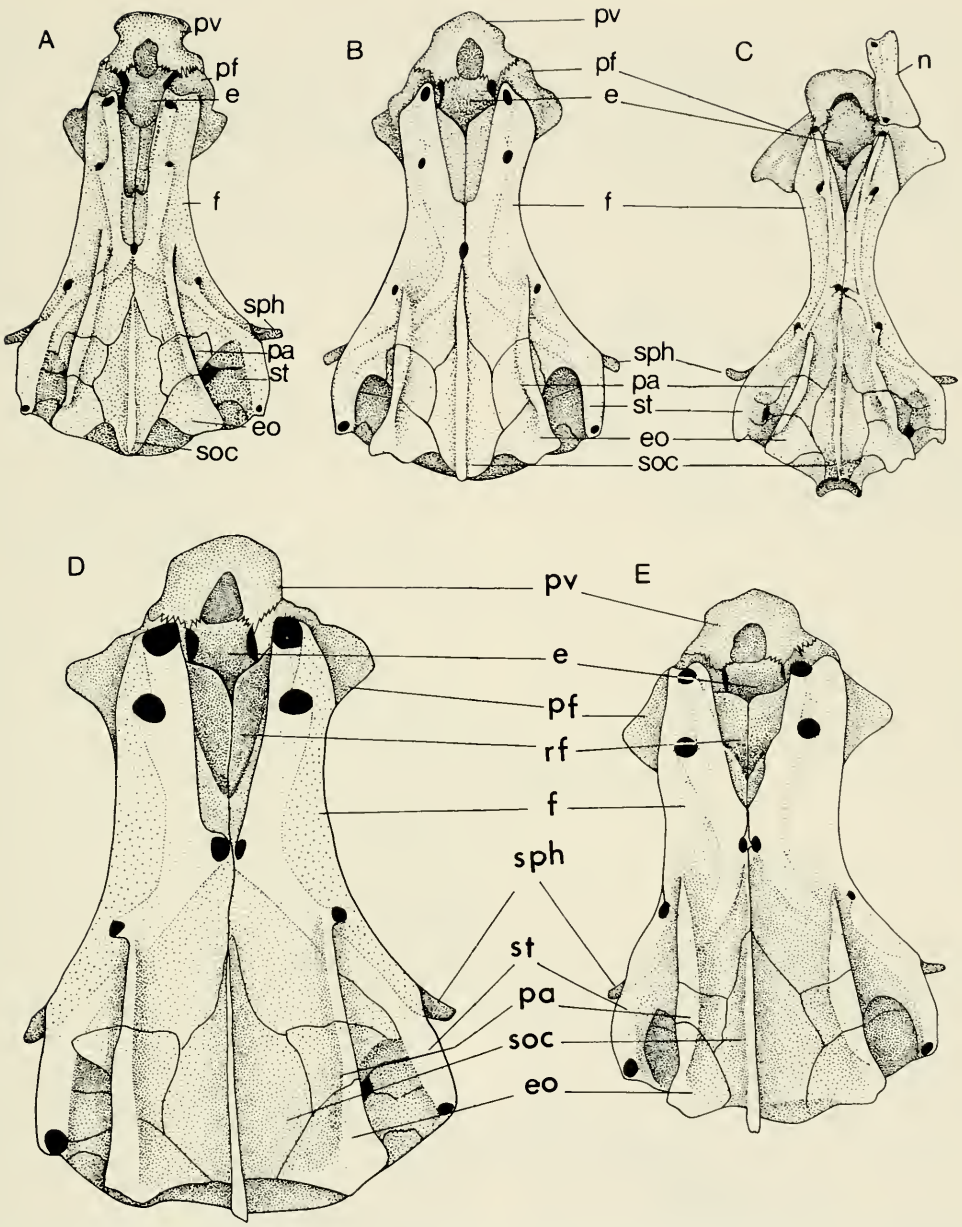

Figure 1. Dorsal aspect of the neurocranium. A, *Ectodus descampsi*; B, *Lestradea perspicax*; C, *Asprotilapia leptura*; D, *Ophthalmotilapia ventralis*; E, *Ophthalmotilapia boops.*

OSTEOLOGICAL ASPECTS OF *ECTODUS*

The neurocranium of *Ectodus* retains many primitive features found in *Astatotilapia ("Haplochromis") burtoni* and *A. elegans* (Liem and Osse, 1975; Barel *et al.*, 1976), such as the somewhat decurved dorsal profile to the preorbital face and the high cranial vault. However, the ethmovomerine region is relatively

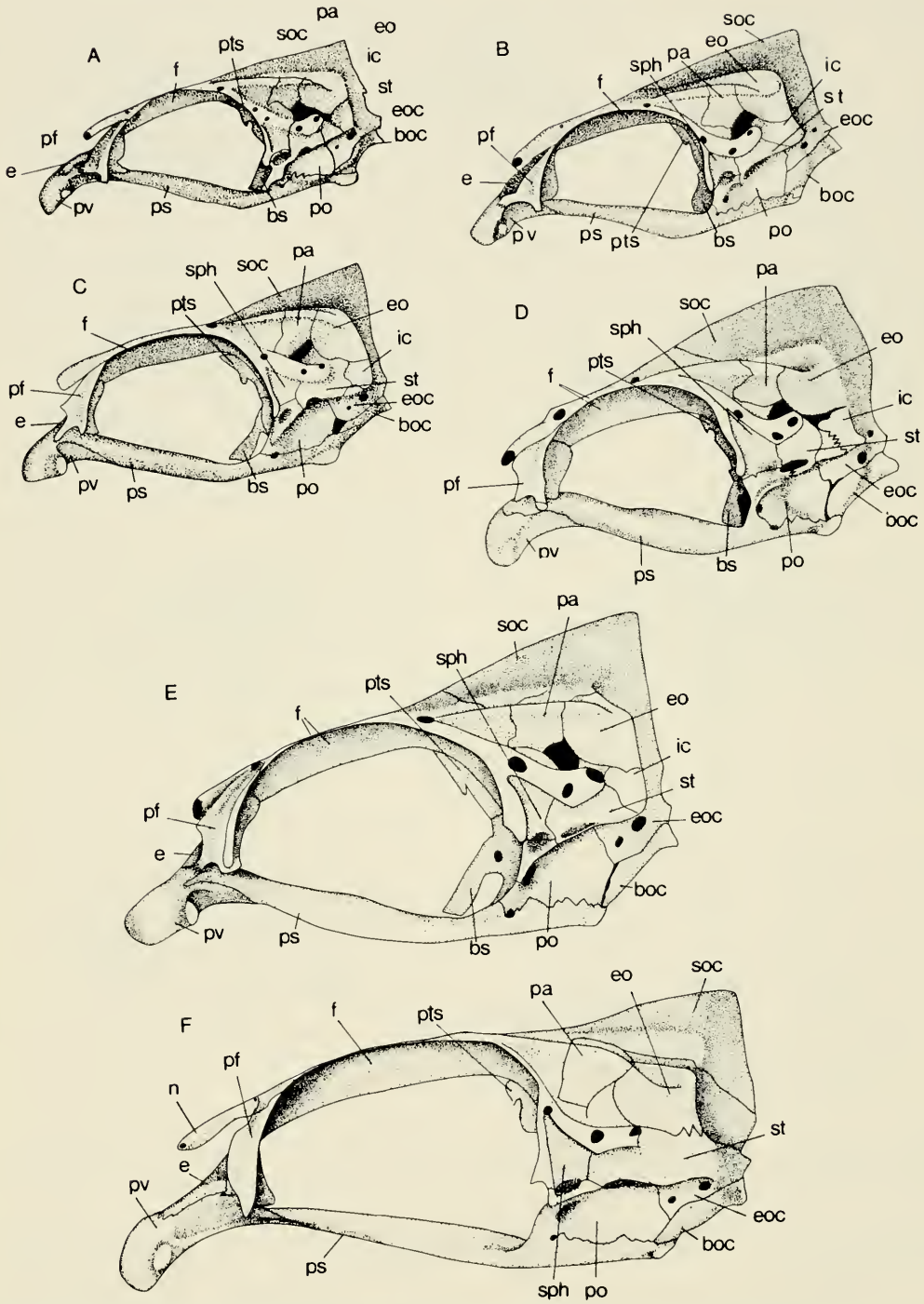

Figure 2. Lateral aspect of the neurocranium. A, *Ectodus descampsi*; B, *Lestradea perspicax*; C, *Cunningtonia longiventralis*; D, *Ophthalmotilapia boops*; E, *Ophthalmotilapia ventralis*; F, *Asprotilapia leptura*.

long and is dorsally differentiated into a well-developed rostral fossa, which is made up by the ethmoid and the depressed anteromedial wings of the frontals (Fig. 1A:e,f). The ethmoid is suturally united with the ascending processes of the vomer and with the lateral ethmoids (Fig. 2A:e,pf). The long axis of the basioccipital makes a 60–70° angle with that of the parasphenoid (Fig. 2). Both the basioccipital and parasphenoid bones contribute to the formation of a prominent pharyngeal apophysis, which is therefore of the *"Haplochromis"* type. Another specialization can be found in the pterosphenoid in the form of a deep notch in the anterior margin of the pterosphenoid (Fig. 2A:pts). The saccular bulla is greatly enlarged (Figs. 2A, 3A).

Morphologically the suspensory apparatus of *Ectodus* deviates from the more generalized configuration of that in *Astatotilapia burtoni* (Fig. 4A; Liem and Osse, 1975). The hyomandibula is slender with an elongate symplectic process and a much reduced flange area below the anterior condyle. The two hyomandibular condyles are distinctly separated, while the symplectic process is connected to the metapterygoid, which is a characteristically shallow bone. The reduced entopterygoid is separated from both the ectopterygoid and the palatine. Half of the entopterygoid's lateral surface is overlapped by the quadrate. The palatine bone is unusual in having its posterior and dorsal border meet at a 90° angle. Posteriorly the suspensory apparatus is delineated by a large preoperculum of which the outer rims of the horizontal and vertical limbs make a distinct 90° angle. The anterior border of the suspensory apparatus formed by the ectopterygoid and the palatine is oblique, making a 60° angle with the horizontal plane.

The jaw apparatus in *Ectodus* (Fig. 4A) possesses a generalized premaxilla resembling that of *Astatotilapia burtoni*, but the maxilla has a prominent earlike postmaxillary process. The elongate, slender mandible is characterized by large, widely separated ascending processes of the dentary and anguloarticular. The ascending process of the anguloarticular is expanded posteriorly to form an adductor fossa, serving as the insertion site of the A_2 part of the adductor mandibulae muscle complex (Fig. 6A:am_2).

The size, shape, and configuration of the opercular apparatus (Fig. 5A) do not differ from those of generalized cichlids. In *Ectodus* the posterodorsal corner of the operculum is raised to form an auricular process, which is not encountered in generalized cichlids.

Of the well-developed five or six circumorbitals, the large lacrimal is distinctly shaped and possesses six sensory pores (Fig. 5A:la). The ventral margin is convex, while the posterodorsal margin is concave. The anterodorsal margin is straight. Anteriorly the lacrimal ends in an anteriorly directed angular process.

The branchial skeleton is not described here because the elements retain a relatively generalized condition and do not contribute to the solution of phylogenetic relationships in this group of cichlids.

MYOLOGICAL ASPECTS OF *ECTODUS*

The lateral head muscles of *Ectodus* (Fig. 6A) retain their unspecialized condition in respect to topography, configuration, and structure. Thus the description of the head muscles of *Astatotilapia elegans* by Anker (1978) also applies to those of *Ectodus*. The adductor mandibulae complex (A_1, A_2, A_3, A_w) of *Ectodus* is identical to that of *A. burtoni*, except that the muscle fibers in the former are considerably more elongate, a feature which is probably correlated with the much larger orbit and the longer and more shallow suspensory apparatus. The levator arcus palatini in *Ectodus* (Fig. 6A:lap) is less voluminous than in *A. burtoni* (Liem and Osse, 1975). Because the hyomandibular flange zone is much more restricted, most of the fibers insert on the

muscular process of the metapterygoid. The other lateral head muscles have not undergone any specialization and will not be described here (Fig. 6A:aap,do,lo,ep).

The ventral muscles of the head of *Ectodus* (Fig. 7A:gh,sh) do exhibit several specializations if compared with those of *A. burtoni* and *A. elegans*. The left and right geniohyoideus anterior (Fig. 7A:gha) are clearly separated, cylindrical muscles, each attaching to the dentary near the mandibular symphysis ventral to the small parallel-fibered intermandibularis. A transverse myosept interrupts the fiber course of the geniohyoideus just anterior to the hyoid symphysis. From the transverse myosept, the geniohyoideus posterior runs laterally to attach to the lateral aspect of the hyoid above the first 2 branchiostegals. The hyohyoideus complex (Fig. 7A:hhs,hhi) lies between the hyoids, the branchiostegals and the medial aspect of the opercular apparatus. We may distinguish three parts: (1) the hyohyoideus inferior (Fig. 7A:hhi) arising from the anteroventral corner of the hyoid ramus runs caudally and slightly lateral to insert on the first to fourth branchiostegal rays by splitting into four heads; (2) the hyohyoideus superior (Fig. 7A:hhs) runs between the rays and the medial aspect of the gill cover; and (3) the hyohyoideus transversus (Fig. 7A:hht) runs between the first left and first right branchiostegals. The hyohyoideus transversus is much better developed than in *A. burtoni*.

In the branchial musculature, the ventral muscles correspond with those of more generalized cichlids (e.g., *Astatotilapia elegans*, Anker, 1978) with respect to topography, structure, attachment sites and shape. Therefore, the description here will be focussed mainly on the dorsal muscles (Figs. 7A, 8A).

Both the levatores externi and interni (Figs. 7A, 8A:le,li) originate from the muscular process of the prootic. The levator internus 1 (or anterior) runs medially and ventrocaudally towards the junction of pharyngobranchials 2 and 3, inserting on both bones. Levator internus 2 (or posterior) passes ventrocaudally along the outer margin of the second pharyngobranchial to insert on the third pharyngobranchial near the junction of the third and fourth epibranchials. The levatores interni are equally developed, cylindrical muscles. The levatores externi 1–3 are relatively slender, straplike muscles running caudoventrally to insert on the dorsal aspects of the epibranchials 1–3 respectively. As in all cichlids (Liem, 1974), the fourth levator externus is the dominant component of the externi complex, lying in a parasagittal plane. Its fibers pass ventrally to converge on the muscular process of the lower pharyngeal jaw. The insertion appears as a complex mixture of muscular and tendinous elements. Only a few lateral fibers attach to the dorsal side of the fourth epibranchial by means of an aponeurotic plate.

The obliquus posterior muscle (Fig. 8A:obp) is characteristically a highly developed muscle in *Ectodus* originating from the dorsal surface of the fourth epibranchial. From this expanded origin, the fibers run laterally and caudoventrally converging on the muscular process of the lower pharyngeal jaw. The insertion site is medial and ventral to that of the fourth levator externus.

Joining the insertion sites of the fourth levator externus and obliquus posterior muscles on the muscular process of the lower pharyngeal jaw is the fifth adductor muscle (Fig. 8A:ad). This spindle-shaped muscle attaches to the medial surface of the dorsal end of the shank of the fourth epibranchial adjacent to its articulation with the fourth ceratobranchial. From this point, the muscle runs ventrally to the muscular process, to which it attaches laterally and posteriorly to the insertion site of the fourth levator externus.

The two transversi dorsales muscles in *Ectodus* (Fig. 8A:tda,tdp) have undergone a reduction as compared with those of *Astatotilapia elegans* (Anker, 1978). Basically, the transversi dorsalis anterior

muscles run between the second pharyngobranchials and the second epibranchials. The drastically reduced transversus dorsalis posterior is a small, straplike muscle which runs between the left and right fourth epibranchials. The fibers run without interruption between the two attachments. As in more generalized cichlids, the transversus dorsalis anterior, although reduced in *Ectodus*, is differentiated into four heads (Anker, 1978). The posterior head (M. transversus epibranchialis 2 pars dorsalis) arises musculously from the dorsal surface of the anterior fork of the second epibranchial and runs medially over the second pharyngobranchial towards a large aponeurosis. Very closely associated with the posterior head is a more ventrally located component (M. transversus epibranchialis 2 pars ventralis) with its attachment to the junction of the second pharyngobranchial and second epibranchial and connecting with the median aponeurosis. The third head (M. transversus pharyngobranchialis 2) is the anterior one, running between the rostromedial surfaces of the left and right pharyngobranchials. Finally, the fourth head (M. cranio-pharyngobranchialis 2) arises from the neurocranium just anterior to the articulation with the first pharyngobranchial, and runs posterolaterally and ventrally to insert on the lateral edge of the anterior aspect of the second pharyngobranchial.

The obliquus dorsalis muscle (Fig. 8A:od) originates from the area lateral to the pharyngeal apophysis of the third pharyngobranchial and runs caudolaterally to insert on both the dorsal aspect of the third epibranchial just medial to the insertion site of the third levator externus and the anterodorsal aspect of the fourth epibranchial.

The large retractor dorsalis muscle (Fig. 8A:rd) runs parasagittally close to the medial plane. Its extensive origin is from the exoccipital, the vertebral bodies of the first three vertebrae, and the apophysis of the third vertebra. From these points, the fibers run anteroventrally to insert musculously on the posterodorsal surfaces of both the third and fourth pharyngobranchials.

Three ventral muscles, the pharyngohyoideus and the pharyngocleithralis externus and internus, play an important role in the operation of the lower pharyngeal jaw (Liem, 1974, 1978). Although none of the three muscles (Fig. 7A:ph,pci,pce) exhibits morphological specializations which can be used in a phylogenetic analysis, they will be briefly described as a basis for future, more functionally focussed studies. As in most cichlids, the fibers of the pharyngohyoideus are interrupted by an aponeurotic sheet halfway along the length of the muscle. Anteriorly, the muscle attaches to the urohyal. Near this insertion site, the left and right pharyngohyoideus merge inseparably into one unit. Posteriorly, the muscle fibers blend into a strong tendon attached to the lateral surface of the anteroventral portion of the lower pharyngeal jaw. The pharyngocleithralis externus arises from the anterolateral surface of the cleithrum from nearly the ventral tip and dorsally until about one-third of its vertical depth. From this origin, the fibers run in a parallel fashion dorsally and slightly anteriorly converging on an aponeurotic system which merges with the insertion tendon of the pharyngohyoideus. However, a subdivision of this aponeurotic system takes up a more lateral course to attach on the fourth epibranchial. The pharyngocleithralis internus originates from a fossa to a point about midway on the vertical depth of the cleithrum; its fibers run anteroventrally to converge on a tendon which inserts on the lower pharyngeal jaw just medial and posterior to the insertion site of the pharyngohyoideus muscle.

COMPARATIVE OSTEOLOGY

Having outlined the main morphological features of the most generalized representative, i.e., *Ectodus*, we can consid-

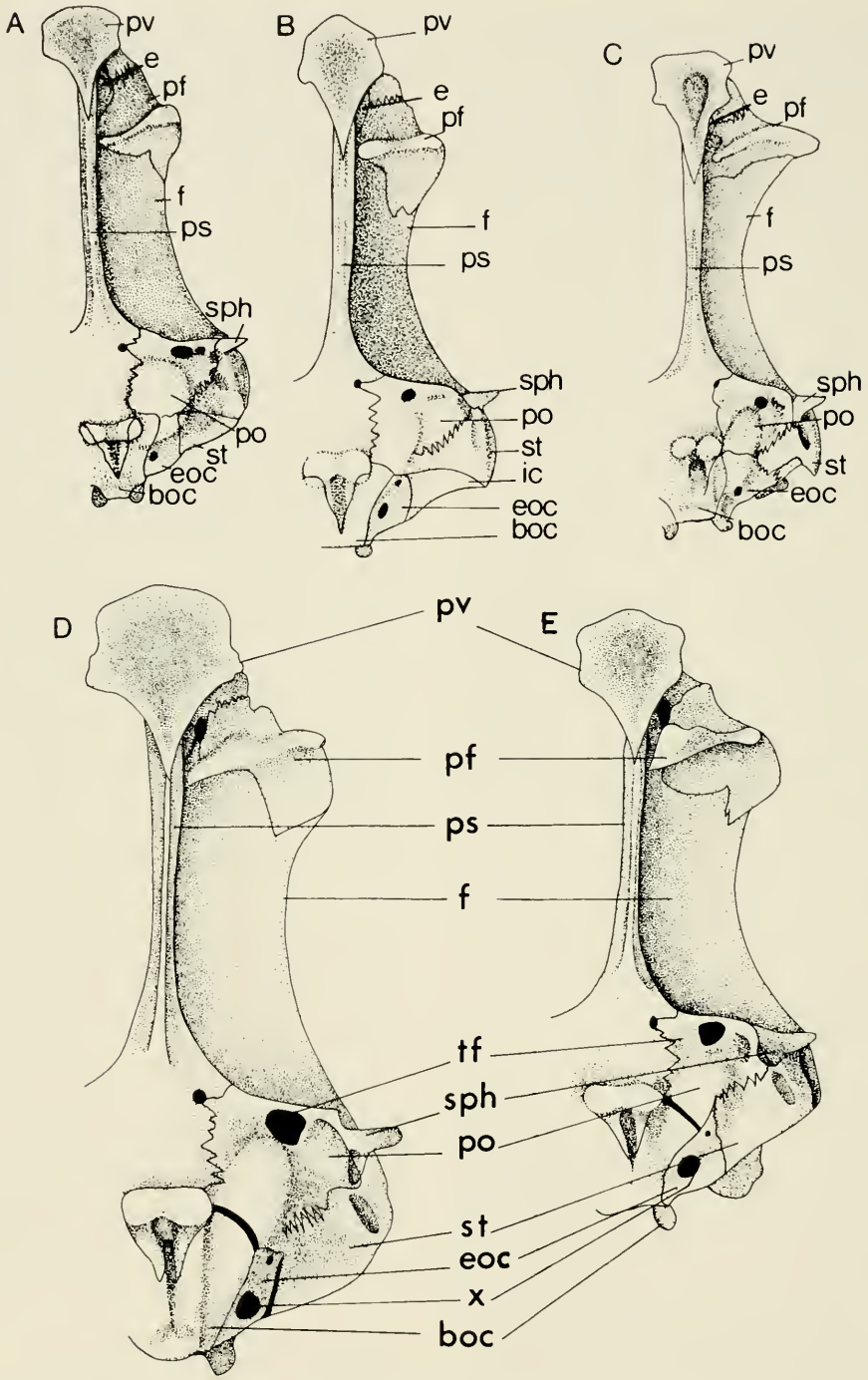

Figure 3. Ventral aspect of the left half of the neurocranium. A, *Ectodus descampsi*; B, *Lestradea perspicax*; C, *Asprotilapia leptura*; D, *Ophthalmotilapia ventralis*; E, *Ophthalmotilapia boops.*

er the anatomy of the other members of the assemblage. The comparative description will not be a comprehensive one. Instead, emphasis will be placed on: (1) features that deviate from those found in *Ectodus*; (2) structural specializations characterizing each genus; and (3) morphological elements which can be used to interrelate the different lineages on a sister group basis.

Neurocranium (Figs. 1, 2, 3). The neurocranium of *Lestradea* is identical to that of *Ectodus* except for a somewhat shorter ethmovomerine complex (Fig. 2B). In *Cunningtonia* the ethmovomerine complex is distinctly shorter, while the basioccipital is excluded from the pharyngeal apophysis (Fig. 2C). The ethmovomerine region in *Ophthalmotilapia* is greatly abbreviated so that the prefrontal is vertically oriented. The neurocrania of *Ophthalmotilapia* and *Ophthalmochromis* resemble each other very closely, both having enlarged sensory canals and foramina. As in *Cunningtonia,* the basioccipital is excluded from the pharyngeal apophysis (Fig. 3C,D,E). However, in *Ophthalmochromis* the abbreviation of the ethmovomerine region is much less pronounced, while the enlargement of sensory canals and foramina is much greater. *Ophthalmochromis* and *Ophthalmotilapia* differ in the orientation of the ventral process of the basisphenoid, being vertical in the latter and oblique in the former (Fig. 2:bs). The most specialized neurocranium is represented in *Asprotilapia*: the ethmovomerine region is elongate with the ethmoid in an almost horizontal position; the lateral ethmoids are enlarged, forming pronounced preorbital processes; the interorbital width is much reduced; the orbit is greatly enlarged; and the sensory canals and foramina are reduced in size.

Opercular apparatus (Fig. 5). The opercular apparatus of all members of this lineage conforms with that of *Ectodus.*

Suspensory apparatus (Fig. 4). The description of the suspensory apparatus for *Ectodus* also applies to the other five genera of this lineage. However, in *Cunningtonia* the palatine is further specialized by the development of a posteriorly directed slender process at the posterodorsal corner. Although the vertical depth of the suspensorium at the level of the metapterygoid is characteristically shallow for all members of this lineage, the feature is least developed in *Ophthalmotilapia* and most pronounced in *Cunningtonia. Cunningtonia* also possesses a very elongate and nearly horizontal symplectic, and the horizontal limb of the preoperculum is longer than the vertical one. In *Ectodus* the horizontal and vertical limbs of the preoperculum are of equal length, while in *Asprotilapia, Lestradea, Ophthalmochromis,* and *Ophthalmotilapia* the horizontal limb of the preoperculum is the shorter one. The sensory canals and pores of the preoperculum are enlarged in *Ophthalmochromis* and *Ophthalmotilapia.*

Jaw apparatus (Fig. 4). As discussed above, the mandible of *Ectodus* is specialized in having an extensive shelflike adductor fossa in the anguloarticular and a laterally expanded ascending process of the dentary. The mandible of *Lestradea, Cunningtonia, Ophthalmochromis,* and *Ophthalmotilapia* exhibits a more generalized configuration with very restricted adductor fossae. The most specialized features are found in the mandible of *Asprotilapia*: the lower jaw is elongate and quite slender, with a drastic reduction in the depth of the unit; the large ascending processes of the dentary and articular are widely separated and form the bulk of the mandible. Morphologically, the premaxillae and maxillae in this lineage are very uniform, resembling those of *Ectodus.* But in *Lestradea* the body of the maxilla is stout, being only as long as the neck and associated condyles, and having a pronounced posteriorly directed postmaxillary process. In general, the ascending processes are shorter than in *Ecto-*

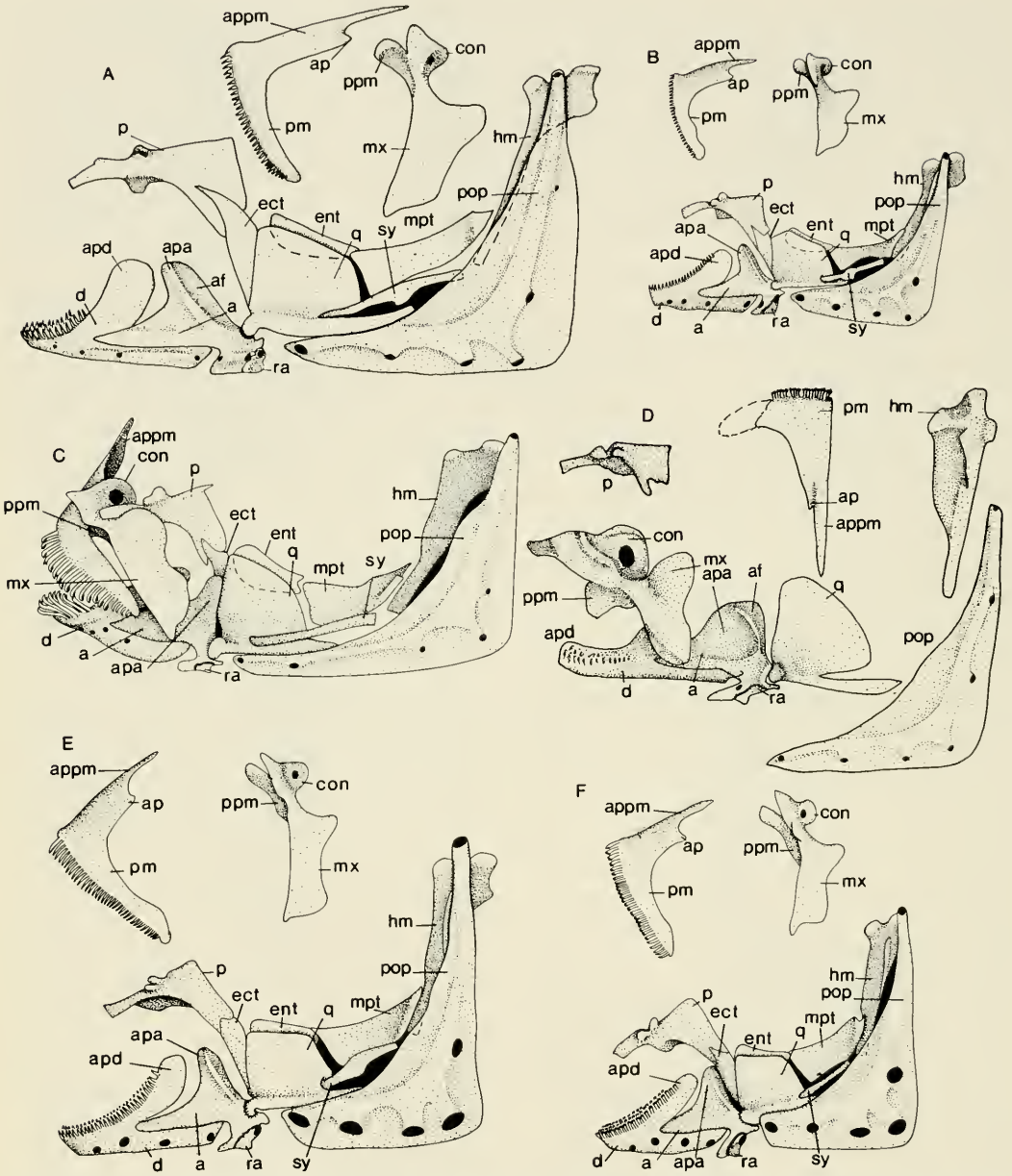

Figure 4. Lateral aspects of the suspensorium, mandible, and upper jaw. A, *Ectodus descampsi*; B, *Lestradea perspicax*; C, *Cunningtonia longiventralis*; D, *Asprotilapia leptura*, in which only parts of the suspensorium are depicted, since the elements have been disarticulated; E, *Ophthalmotilapia ventralis*; F, *Ophthalmotilapia boops*.

dus. However, both the premaxilla and maxilla in *Asprotilapia* (Fig. 4D) exhibit several unique specializations. In the premaxilla, the articular process is reduced and shifted into a more forward position. The shape of the shortened maxilla deviates greatly from that of other cichlids. The greatly enlarged cranial

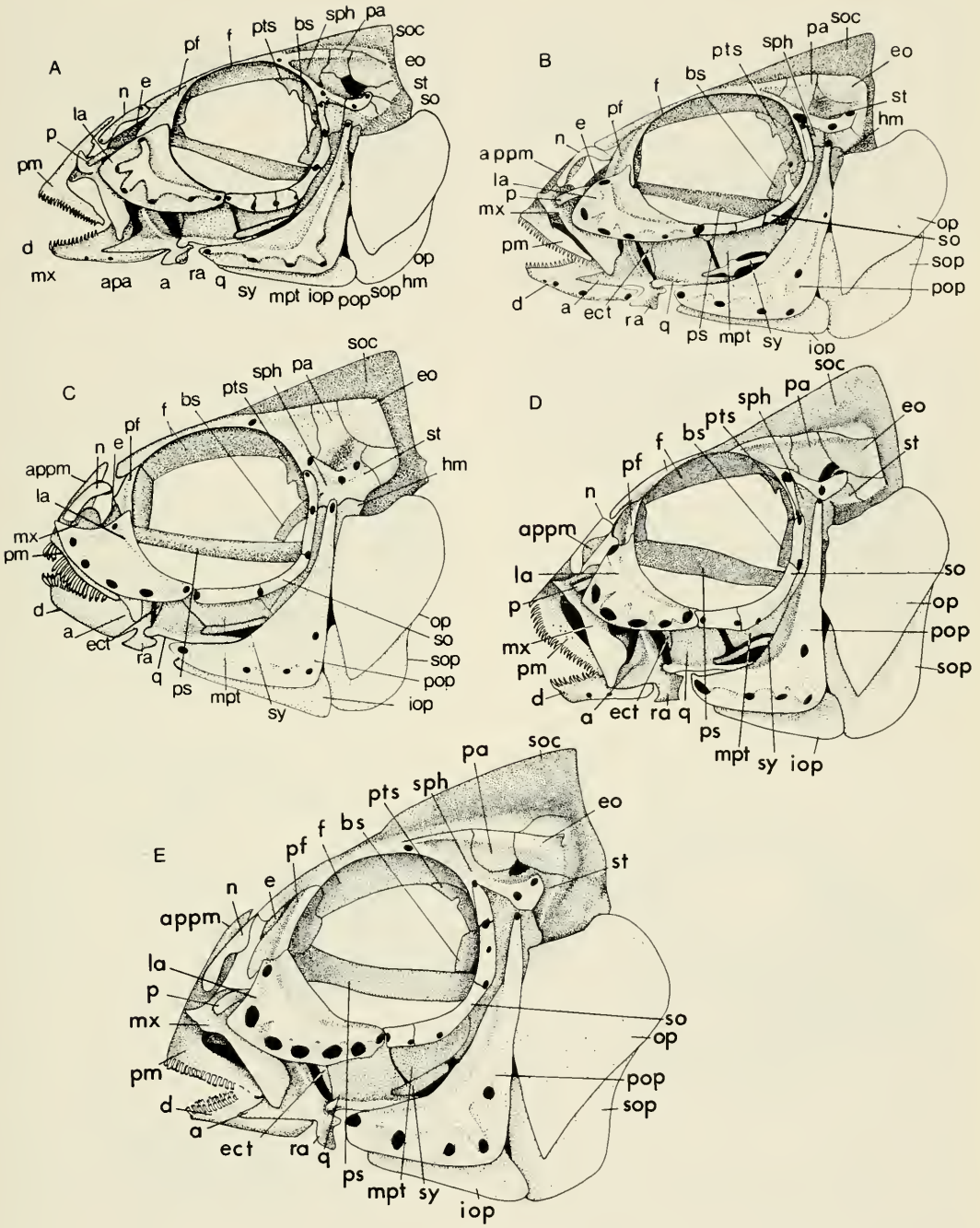

Figure 5. Lateral aspect of the skull. A, *Ectodus descampsi*; B, *Lestradea perspicax*; C, *Cunningtonia longiventralis*; D, *Ophthalmotilapia ventralis*; E, *Ophthalmotilapia boops*.

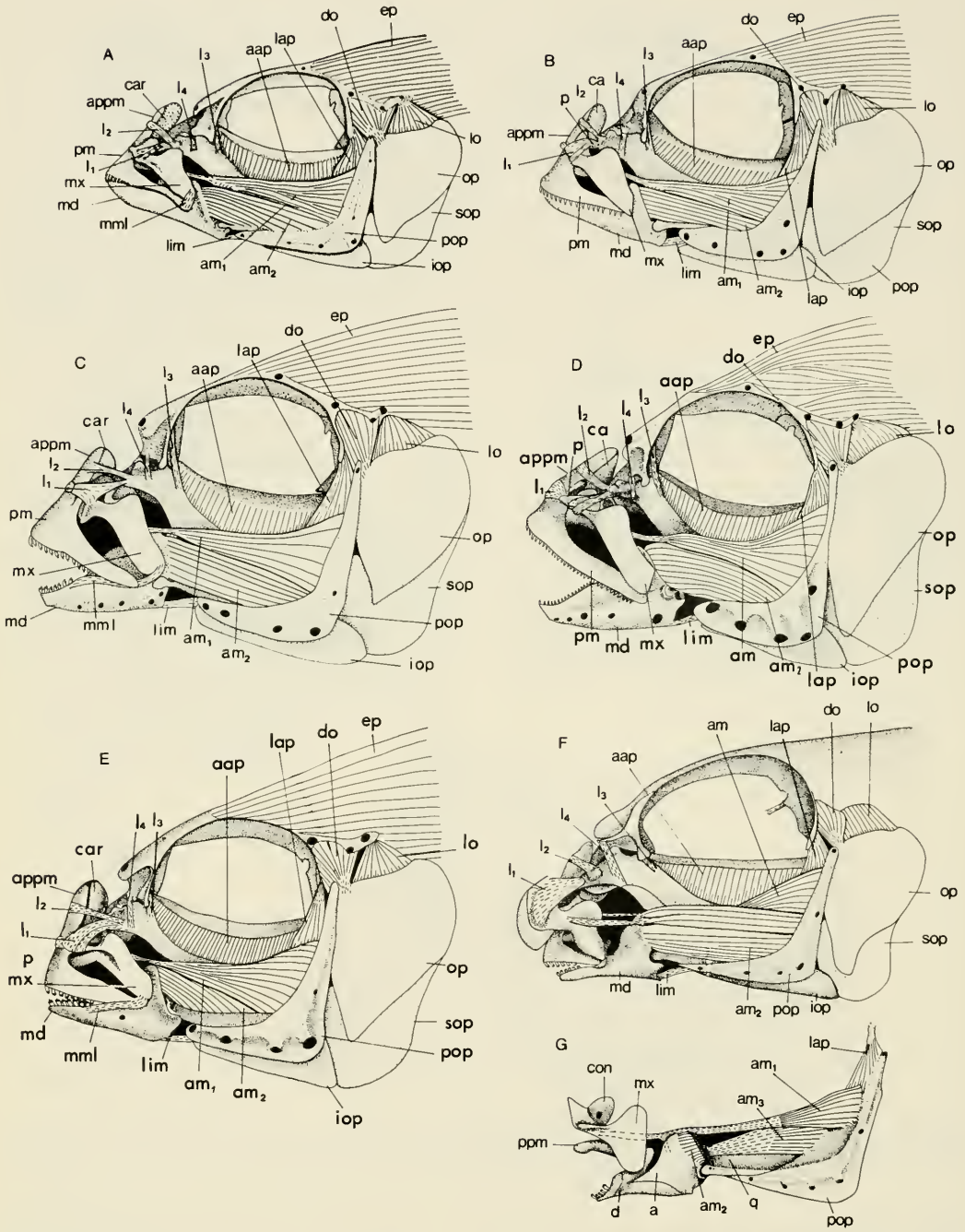

Figure 6. Lateral aspect of the cephalic musculature after removal of the lacrimal, circumorbitals, and eyes. A, *Ectodus descampsi*; B, *Lestradea perspicax*; C, *Cunningtonia longiventralis*; D, *Ophthalmotilapia ventralis*; E, *Ophthalmotilapia boops*; F, *Asprotilapia leptura*; G, deeper dissection of the adductor mandibulae complex after removal of part A_2 in *Asprotilapia*.

condyle and premaxillary process constitute the bulk of the bone, with its dorsal extremity directed anteriorly as a flattened process. The angle between the body of the maxilla and the part bearing the cranial condyle and premaxillary process is more acute than that of other members of the lineage.

Dentition. Much of cichlid classification and phylogeny has been based solely on dental characters. In this lineage dental characters are of little value in establishing phyletic relationships at the generic level, because the polarity of character transformation is not known, and intraspecific and ontogenetic plasticity further complicates the use of dental characters. No new information is added here to our already extensive knowledge on the teeth of members of this lineage (Poll, 1943; Poll and Matthes, 1962). In *Ectodus descampsi* the teeth are conical and arranged in two to three rows in such a fashion that the outer rows on the lower jaw are directed outward. *Lestradea perspicax perspicax,* a subspecies from the northern half of Lake Tanganyika, possesses conical teeth arranged in three to four rows. The teeth of the outer row are much larger and are directed outward. In juveniles of *L. perspicax stappersi* the teeth are invariably tricuspid, while in the adult all teeth can become conical. *Cunningtonia, Ophthalmochromis,* and *Ophthalmotilapia* have teeth with long flexible stalks, giving them a mobile nature, which is regarded as an adaptation to raking and scraping algae off irregular rock surfaces. In *Cunningtonia* the tricuspid teeth are numerous, forming a broad band in each jaw. Characteristically, the distal end of each tooth is bent backwards rather sharply. In *Ophthalmotilapia* most teeth are tricuspid throughout the life history of the fish, except for the conical ones toward the outer corners of the jaws. It is remarkable that the dental patterns in the subspecies of *Lestradea* closely parallel those in the subspecies of *Ophthalmochromis. Ophthalmochromis ventralis ventralis* is a conical-toothed form, geographically restricted to the northern half of Lake Tanganyika. In the southern subspecies, *Ophthalmochromis ventralis heterodontus,* the juveniles have tricuspid teeth, while later in development a mixed dentition of tricuspid and conical teeth appears. *Asprotilapia* has small teeth with very long slender stalks and expanded tricuspid crowns arranged in two rows.

COMPARATIVE MYOLOGY

The lateral head musculature in members of this lineage is relatively uniform (Figs. 6, 7, 8). The description given for *Ectodus* also applies to other members of the lineage except for *Asprotilapia,* which exhibits many unique specializations in the lateral head musculature. In *Asprotilapia* (Fig. 6F,G) the elongate adductor mandibulae part A_2 is the dominant muscle occupying the greater part of the cheek region. From their origin on the preoperculum, the fibers run parallel to insert on the extensive adductor fossa of the mandible. Part A_1 of the adductor mandibulae complex in *Asprotilapia* is a small muscle originating from the preoperculum and symplectic processes of the hyomandibula; its fibers insert on a tendon at a point about halfway between origin and insertion. Thus the tendon of part A_1 is exceptionally long; just beyond the ascending process of the articular it gives off a ventral branch which merges with the tendon of the intramandibular (A_w) part of the adductor mandibulae complex. The A_1 tendon inserts on the medial aspect of the maxilla in the area between the cranial condyle and premaxillary process. The adductor mandibulae complex of *Lestradea, Cunningtonia, Ophthalmochromis,* and *Ophthalmotilapia* deviates from that of *Ectodus* in the dominance of the A_1 part. Both in cross-sectional area and in volume, the A_1 is the largest component of the complex (Fig. 6).

The configuration of the remaining lateral head muscles and the ventral head

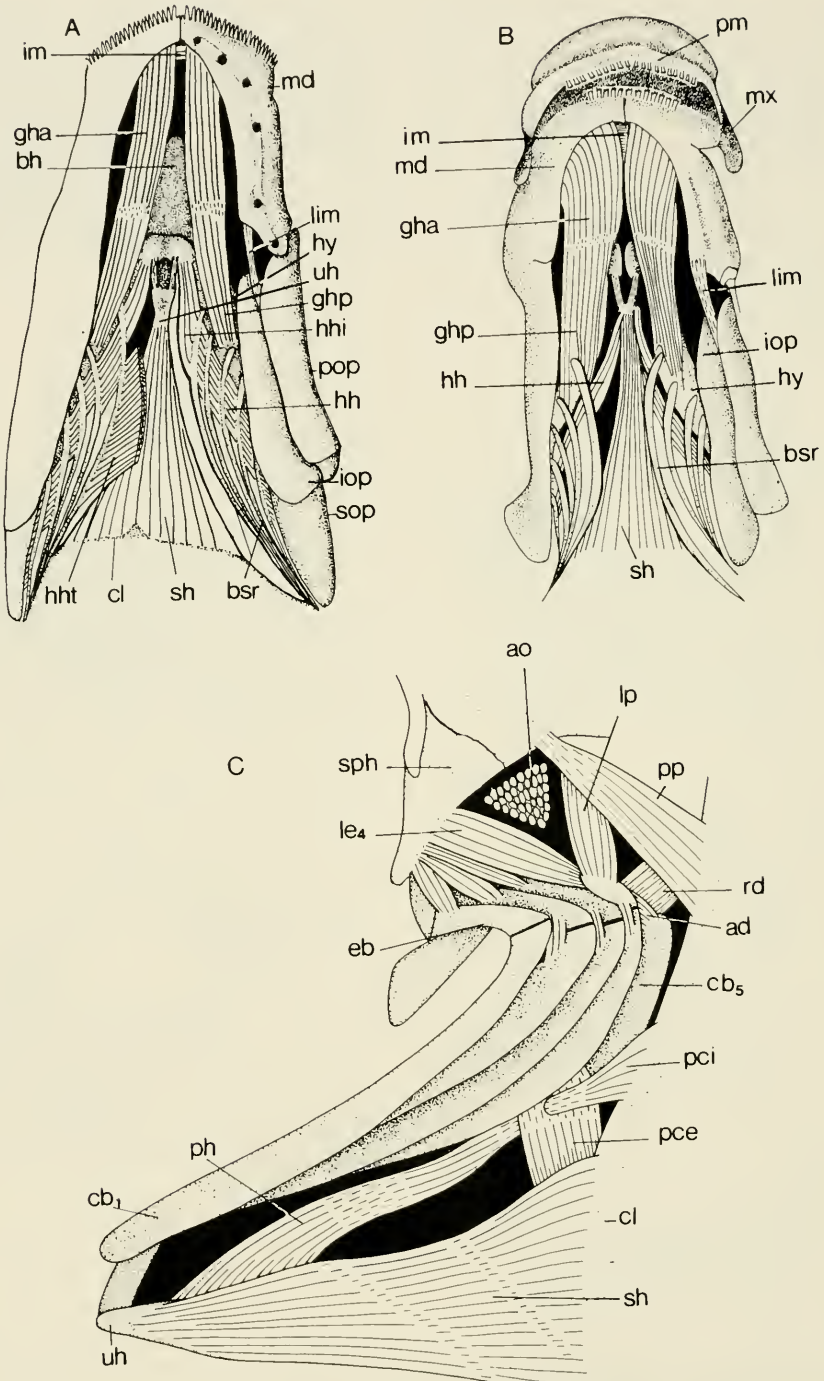

Figure 7. Ventral aspect of the ventral cephalic musculature with the hyohyoideus transversus partially or in B, entirely removed. A, *Ectodus descampsi*; B, *Asprotilapia leptura*; C, lateral view of the branchial musculature after removal of the gills and mucous membranes in *Ophthalmotilapia nasutus*.

muscles in all members of this lineage conforms with that of *Ectodus* (Fig. 6).

In general, the branchial musculature of members of this lineage resembles that of *Ectodus* (Figs. 7, 8). In *Asprotilapia* the transversus dorsalis anterior muscles have been reduced to only one head, running between the 2nd pharyngobranchials (Fig. 8C:tda). *Ophthalmotilapia* exhibits two specializations in the dorsal branchial musculature: both the obliquus dorsalis and retractor dorsalis are greatly enlarged and are subdivided into two distinct heads (Fig. 8D:od,rd).

PHYLETIC ANALYSIS

Although an in depth study on phyletic relationships is not yet available, it is generally accepted that the endemic lacustrine cichlids of Lake Tanganyika have been derived from several unrelated fluviatile lineages. The fluviatile genera "*Tilapia*," *Tylochromis*, "*Haplochromis*," and *Lamprologus* are considered the primitive sister lineages of the many derived lineages of endemic cichlids in Lake Tanganyika (e.g., Regan, 1920; Fryer and Iles, 1972). Unfortunately, no attempts have been made to interrelate the different lineages within Lake Tanganyika on a sister group basis. Since the phyletic relationships of the lacustrine lineages are still poorly known, the determination of their sister group interrelationships with the more generalized fluviatile lineages will be postponed until a much broader data base is available. Without the information on the relationships of the lacustrine species and their respective fluviatile sister lineages, it is impossible to make precise outgroup comparisons. Despite these limitations, it is possible to construct a classification from which a theory of relationships is recoverable. Clearly its precision and efficiency can be improved, but that must await a phyletic analysis of fluviatile taxa.

In this phyletic analysis comparisons have been made between the lacustrine assemblage *Asprotilapia, Ectodus, Lestradea, Cunningtonia, Ophthalmochromis,* and *Ophthalmotilapia* and the fluviatile taxa *Astatotilapia burtoni* and *Sarotherodon nilotica. Tylochromis, Sarotherodon, Tilapia,* and *Lamprologus* are specialized along very different lines (Liem, in prep.) and are not closely related to the *Ophthalmotilapia* lineage. Although an outgroup comparison is tentative, I have considered the morphology of *A. burtoni* to be generalized (Liem, in prep.) and therefore representative of a plesiomorphous group with which the apomorphous *Ophthalmotilapia* assemblage can be compared. In the succeeding phyletic analysis I have made the basic assumption that the morphological condition of the various structures in *Astatotilapia burtoni* and *A. elegans* represents the primitive state. Any deviations from this basic morphological configuration are considered specializations. Monophyletic lineages are then formulated on the basis of shared specialized characters.

THE *OPHTHALMOTILAPIA* ASSEMBLAGE AS A MONOPHYLETIC LINEAGE

A comparison of the osteology and myology of all cichlid genera of Lake Tanganyika and the four fluviatile species *Sarotherodon nilotica, Astatotilapia burtoni, Tylochromis microlepis,* and *Lamprologus congolensis* has resulted in the identification of a suite of eight derived characters shared by *Asprotilapia, Ectodus, Lestradea, Cunningtonia, Ophthalmochromis,* and *Ophthalmotilapia.* This group of genera will be referred to as OA (*Ophthalmotilapia* Assemblage) in the following discussion.

The entopterygoid is separated from the palatine in the OA (Fig. 4:ent). In generalized cichlids the entopterygoid is attached to the posterior margin of the body of the palatine (Goedel, 1974; Vandewalle, 1972; Liem and Osse, 1975; Barel *et al.,* 1976) or the two elements abut against each other. A similar connection is also present in several special-

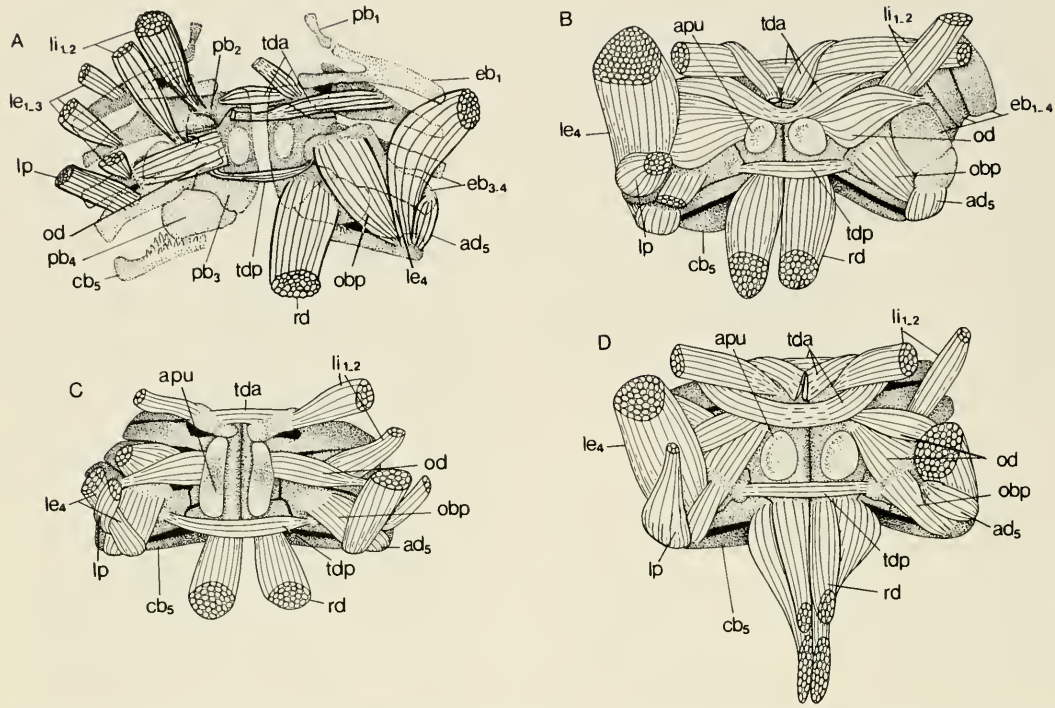

Figure 8. Dorsal aspect of the branchial musculature. A, *Ectodus descampsi*, in which the dissection has been carried out in greater detail to show the precise insertions and origins of the muscles; B, *Lestradea perspicax*; C, *Asprotilapia leptura*; D, *Ophthalmotilapia boops*.

ized lineages of Lake Tanganyika, such as the herbivores (e.g., *Simochromis* and *Petrochromis*), piscivores (Liem, 1978), scale eaters (Liem and Stewart, 1976) and invertebrate pickers (Liem, 1979). Separation of the palatine and the entopterygoid (Fig. 4:ent,p) is considered as a derived character state. This specialization also occurs in *Xenotilapia* (Liem and Osse, 1975), *Aulonocranus, Callochromis*, and *Cardiopharynx* indicating the possibility that these genera are related to the OA. However, on the basis of the present data it is impossible to ascertain that *Xenotilapia, Aulonocranus, Callochromis*, and *Cardiopharynx* are members of a sister lineage of the OA.

The functional significance of the separation of the entopterygoid from the palatine remains unclear, because no correlation can be found between this specialized feature and specializations in either the mobility and shape of the suspensorium and jaws, or the morphological characteristics of the adductor mandibulae complex.

A unique specialization of the OA can be found in the palatine bone (Fig. 4E,F:p). The dorsal margin and the vertically directed posterior border of the palatine meet at a 90° angle. Because the palatine is expanded in the region of this 90° angle, it has a characteristic shape when viewed laterally (Fig. 4:p). The 90° posterodorsal angle surmounting a posterodorsal expansion of the palatine is not found in any of the other Lake Tanganyika cichlids and deviates from the condition in generalized cichlids (e.g., *Astatotilapia burtoni*, Liem and Osse, 1975; *A. elegans*, Barel *et al.*, 1976). This uniquely specialized shape of the pala-

tine is found in all members of the OA, indicating that the group may represent a monophyletic lineage.

The hyomandibula of cichlids exhibits remarkable diversity in shape and size. However, among the diverse forms one can recognize distinct themes, each of which may reflect a particular ancestry. The hyomandibula of *Astatotilapia burtoni* (Liem and Osse, 1975) and *A. elegans* (Barel *et al.*, 1976) is characteristically stout, with an expanded flange associated with the relatively short symplectic process. In *Tilapia* and *Sarotherodon* (Vandewalle, 1972; Goedel, 1974) the symplectic process is elongate and the hyomandibular flange below the anterior head is only moderately developed. Both *Lamprologus* and *Tylochromis* possess a strongly modified hyomandibula. The slender hyomandibula of all members of the OA (Fig. 4:hm) resembles that of *Tilapia,* but it has a relatively longer symplectic process, and has lost its flange. However, a reduced flange is present in *Asprotilapia.* Because the specialization of the hyomandibula in members of the OA has progressed further than in *Tilapia,* the feature is considered derived and indicative of the monophyletic nature of the group. A similarly specialized hyomandibula is found in *Xenotilapia.*

The anterior margin of the pterosphenoid in members of the OA is peculiarly notched (Fig. 2:pts). A liplike process at the base of the notch serves as the origin of a strong ligament which attaches to the eye ball. Although the notched anterior margin of the pterosphenoid and the associated ligament occurs in some other specialized cichlids, it is absent in the generalized forms. The presence of the pterosphenoid notch in all members of the OA is considered as supporting evidence for the hypothesis of monophyly of the OA.

All members of the OA possess a very shallow suspensory apparatus at the level of the metapterygoid (Fig. 4). This specialization is the result of a sharp decrease in the vertical depth of the metapterygoid, which in all generalized cichlids has a much greater vertical depth. Actually among Lake Tanganyika cichlids this specialization and the peculiar position of the ectopterygoid is characteristic of the OA assemblage.

Although the presence of a well-developed auricular process (Fig. 5:op) on the operculum occurs in several specialized cichlid groups, the character is here included in the suite of derived characters, upon which the hypothesis of monophyly of the OA is based.

Two myological specializations in the branchial musculature of all members of the OA offer further evidence for the probable monophyletic nature of the group. In sharp contrast to the condition in generalized cichlids, there is a clear reduction in the development of the transverse dorsalis muscle accompanied by a hypertrophy of the obliquus posterior muscle (Fig. 8:obp). Reduction of the transversus dorsalis and hypertrophy of the obliquus posterior have not been found in *Astatotilapia elegans* (Anker, 1978) and other groups of specialized cichlids in Lake Tanganyika. In view of this admittedly tentative evidence, the reduction of the transversus dorsalis and hypertrophied obliquus posterior are considered derived characters supporting the notion that the OA is actually monophyletic.

The OA is viewed as a monophyletic lineage (Fig. 9: cladogram of synapomorphies [1]–[30]) because its members share the following suite of characters:

(1) The entopterygoid is widely separated from the palatine.
(2) The posterior and dorsal margins of the palatine form a 90° angle.
(3) The slender hyomandibula has a long symplectic process and no or a very reduced hyomandibular flange.
(4) The anterior margin of the pterosphenoid is notched.
(5) The vertical depth of the metapterygoid is shallow.

(6) The operculum has a distinct auricular process.
(7) The transversus dorsalis is reduced.
(8) The obliquus posterior is enlarged.

No other cichlid in Lake Tanganyika possesses this suite of derived characters, although none of the above mentioned characters, with the possible exception of (2), is autapomorphic. The sister group of the *Ophthalmotilapia* lineage is still unknown. Possibly, *Xenotilapia, Callochromis,* and *Aulonocranus* may represent members of a sister group of the *Ophthalmotilapia* lineage since they do share two of the above mentioned derived characters (i.e., [1] and [3]). However, the precise relationships of this lineage to others must await more data and further analysis now in progress.

This phyletic hypothesis for the existence of an *Ophthalmotilapia* lineage differs from the previous hypotheses (Fryer and Iles, 1972, and Regan, 1920) by the inclusion of *Ectodus.* In the previous schemes, *Ectodus* has been regarded as a derivative of a "*Haplochromis*" or "*Haplochromis*-like" ancestor, while the other members of the *Ophthalmotilapia* lineage were seen as derivatives of "one or more unknown ancestors," which are not related to "*Haplochromis.*" Unfortunately the inferred relationships of the relevant genera in the previous hypotheses have been presented with virtually no documentation, and were not based on Hennigian methodology.

Phyletic Relationships of Members of the *Ophthalmotilapia* Lineage

The proposed phyletic relationships are depicted in the cladogram in Fig. 9. Two major lineages are recognized: one contains the monotypic genus *Asprotilapia,* and the second lineage contains the five remaining genera. The following discussion deals first with the synapomorphies for the entire complex, and then with those derived characters that distinguish subunits of decreasing levels of universality within the assemblage.

Asprotilapia represents a very specialized lineage, with six autapomorphic characters:

(9) The elongate, slender mandible has an expanded adductor fossa (Fig. 9:9) serving as the insertion site for the adductor mandibulae part A_2 (Fig. 6F,G).
(10) The posterior head of the transversus dorsalis anterior is absent (Figs. 9:10, 8C:tda).
(11) The lateral ethmoids are greatly enlarged (Figs. 1C, 3C:pf).
(12) The interorbital width of the neurocranium is drastically reduced (Fig. 1C).
(13) The reduced articular process of the premaxilla is in a more forward position (Fig. 4D:ap).
(14) The greatly enlarged cranial condyle and the premaxillary process constitute the bulk of the maxilla (Fig. 4D:cc,pmp).

The rare species *Asprotilapia leptura* represents a highly specialized lineage, with a very elongate body and a much attenuated caudal region. Because of the ventral mouth and the tricuspid teeth arranged in two series on both jaws, *Asprotilapia* is considered herbivorous, feeding primarily on epilithic algae.

The remaining five genera are regarded as a monophyletic group on the basis of their sharing two derived characters:

(15) Anteriorly the enlarged lachrimal is differentiated into a distinct process (Figs. 9:15, 5:la). The blunt process is directed anteroventrally, except in *Cunningtonia* in which it is directed anterodorsally.
(16) The adductor mandibulae part A_1 has become the dominant component of the adductor mandibulae complex (Fig. 6:am_1). Its cross-sectional area surpasses that of the other parts. The origin from the preoperculum has expanded ventrally

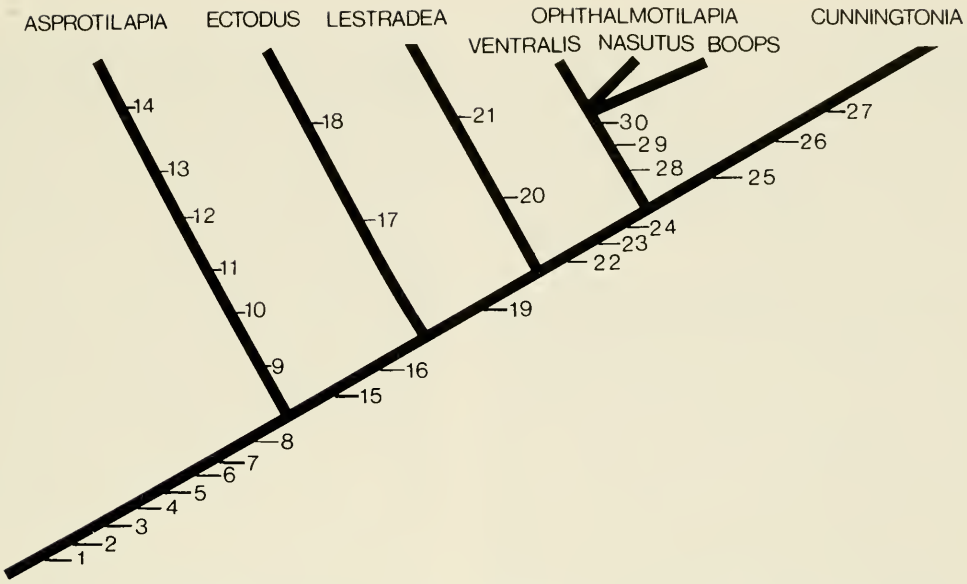

Figure 9. Proposed cladogram depicting the phylogenetic relationships of the *Ophthalmotilapia* lineage on the basis of the following synapomorphies: (1) entopterygoid separated from palatine; (2) posterior and dorsal margins of palatine form a 90° angle; (3) slender hyomandibula with long symplectic process and reduced hyomandibular flange; (4) anterior margin of pterosphenoid notched; (5) vertical depth of metapterygoid shallow; (6) operculum with auricular process; (7) transversus dorsalis muscle reduced; (8) obliquus posterior muscle enlarged; (9) elongate, slender mandible with expanded adductor fossa; (10) transversus dorsalis anterior absent; (11) prefrontals greatly enlarged; (12) interorbital width greatly reduced; (13) reduced articular process of premaxilla in forward position; (14) cranial condyle and premaxillary process of maxilla greatly enlarged; (15) lacrimal enlarged with a distinct anterior process and elaborate sensory system; (16) adductor mandibulae part A_1 is dominant; (17) saccular bulla enlarged; (18) horizontal and vertical limbs of preoperculum of equal length; (19) elongate gut which is at least 2.5 times the fish's standard length; (20) edentulous anterior process of the lower pharyngeal jaw is only half as long as the toothed part; (21) stout body of maxilla with prominent postmaxillary process; (22) jaw teeth mobile with long stalks; (23) first pelvic fin ray is greatly elongate; (24) straight vertical limb of preoperculum forms a 90° angle with horizontal limb; (25) symplectic elongate; (26) a spinelike process at junction of dorsal and posterior margins of palatine; (27) long-stalked tricuspid jaw teeth with posteriorly recurved crowns; (28) distal end of elongate first ray uniquely bifid and widened into spatulae; (29) trend toward enlarged sensory canals and pores; (30) hypertrophied retractor dorsalis muscle subdivided into two distinct heads.

at the expense of the adductor mandibulae part A_2.

Ectodus inhabits shallow waters of sandy areas, feeding on a mixed diet of insect larvae, crustaceans, and filamentous algae. According to the present phylogenetic hypothesis, *Ectodus* represents the most primitive of the *Ophthalmotilapia* lineage. Two autapomorphies distinguish *Ectodus* from the other genera:

(17) The saccular bulla is greatly enlarged (Figs. 2, 3).
(18) The horizontal and vertical limbs of the preoperculum are of equal length (Figs. 4, 5:pop).

The next monophyletic subunit is composed of *Lestradea*, *Ophthalmotilapia*, *Ophthalmochromis*, and *Cunningtonia*, which all share one notable feature:

(19) The gut is elongate and is at least 2.5 times the fish's standard length.

Lestradea possesses a gut which is 2.5–4 times the standard length. In *Ophthalmotilapia* and *Ophthalmochromis* the gut measures 3–3.5 times the standard length. The longest gastrointestinal tract is that of *Cunningtonia*, measuring 5–6 times the fish's standard length. The relative increase in the length of the digestive tract is correlated with an increased emphasis on a herbivorous diet.

Within this subunit, *Lestradea* can be

distinguished by two autapomorphic characters:

(20) The edentulous anterior process of the lower pharyngeal jaw is only half as long as the toothed part.
(21) The body of the maxilla is stout and has a prominent postmaxillary process (Fig. 4).

Cunningtonia, Ophthalmochromis, and *Ophthalmotilapia* form a distinct subunit sharing three specialized characters:

(22) The jaw teeth have long stalks and are mobile.
(23) The first pelvic fin ray is greatly elongate.
(24) The posterior margin of the vertical limb of the preoperculum is straight and forms a 90° angle with that of the horizontal limb (Fig. 4).

Within this monophyletic subunit, *Cunningtonia* possesses three autapomorphic features:

(25) The symplectic is very elongate, lengthening the suspensorium (Fig. 4:sy).
(26) At the 90° junction of the dorsal and posterior margins of the palatine is a spinelike process directed dorsoposteriorly (Fig. 4:p).
(27) The long-stalked tricuspid jaw teeth have posteriorly recurved crowns (Fig. 6).

Finally, the close relationship of *Ophthalmochromis* and *Ophthalmotilapia* can be established on the basis of three derived characters:

(28) The distal end of the very elongate first ray of each pelvic fin in the male is uniquely bifid and widened into spatulae.
(29) All members of this subunit show a trend toward enlargement of the sensory canals and pores of the head (Figs. 1, 2, 5).
(30) The hypertrophied retractor dorsalis is subdivided into two distinct heads (Fig. 8:rd).

The genus *Ophthalmochromis* was established by Poll (1956) on the basis of *O. ventralis,* its type species possessing conical teeth in adults as well as juveniles. *Ophthalmotilapia boops,* on the other hand, has mainly tricuspid teeth, although conical teeth are present on the posterolateral corner of the jaws. The neurocranium of *O. boops* has a shorter ethmovomerine region and a steeper ethmovomerine slope than that of *Ophthalmochromis ventralis.* However, the condition with respect to the ethmovomerine region in the skull of *Ophthalmochromis nasutus* is intermediate between that of *boops* and *ventralis.* The validity of *Ophthalmochromis* and *Ophthalmotilapia* as distinct genera is questionable.

Originally the distinction between *Ophthalmochromis* and *Ophthalmotilapia* was based on morphological gaps in the general and skull morphology. With the discovery of *Ophthalmochromis nasutus,* the few morphological gaps of characters in the skulls of *ventralis* and *boops* are bridged. *Ophthalmochromis nasutus* has an ethmovomerine slope intermediate between those of *ventralis* and *boops.* The subtle differences in the decurvature of the skull anteriorly between *Ophthalmochromis* and *Ophthalmotilapia* are well within the range found intragenerically in *Perissodus* (Liem and Stewart, 1976). In the related genus *Lestradea,* the contrast between tricuspid and conical teeth has been interpreted to indicate a difference at the subspecies level for, respectively, *L. perspicax stappersi* and *L. perspicax perspicax.* In *Lestradea* tooth shape changes ontogenetically from tricuspid to bicuspid and conical. In *ventralis, nasutus,* and *boops* geographical variation has been demonstrated very convincingly (Poll and Matthes, 1962). Conical teeth do occur in all species, even though in *boops* the tricuspid form is dominant. In view of the fact that tooth form in some members of this lineage can change drastically from tricuspid to conical during ontogeny, and that conical teeth actually

occur in all forms varying only in relative abundance, the presumed "morphological gap" between *ventralis* and *nasutus* on the one hand, and *boops* on the other hand, is nonexistent and does not justify the recognition of two genera.

More importantly, the phylogenetic relationships as depicted in Fig. 9 indicate that *ventralis*, *nasutus*, and *boops* share a recent common ancestor not shared by any of the other taxa. I propose, therefore, that *Ophthalmotilapia* and *Ophthalmochromis* be considered synonyms. The name *Ophthalmotilapia* established by Boulenger in 1901 has priority over *Ophthalmochromis* (Poll, 1956).

"ADAPTIVE RADIATION" OF THE *OPHTHALMOTILAPIA* LINEAGE

Once the phyletic nature and relationships of the *Ophthalmotilapia* lineage have been established, a more meaningful statement can be made concerning their adaptive radiation.

Unlike most cichlid lineages, the radiation in the *Ophthalmotilapia* lineage especially has involved behavioral patterns in courtship and specific recognition signals, although the feeding apparatus does exhibit some morphological diversity. All are oral brooders, but in *Cunningtonia* and *Ophthalmotilapia* the pelvic fins of the males are drawn out into long slender filaments whose tips reach posteriorly to the margin of the anal fin and terminate in brightly colored spots which function not only for species recognition, but probably also as egg dummies (Fryer and Iles, 1972: 110, 121). The strikingly colored tips of the elongated pelvic fins play an important role in specific, and, thus inevitably, in sex recognition in the complex communities where *Cunningtonia* and *Ophthalmotilapia* occur. Both *Cunningtonia* and *Ophthalmotilapia* produce only a few eggs, measuring 3.5–4 mm in diameter. Egg collecting precedes fertilization. *Ectodus*, the most primitive member of the lineage, and *Lestradea* produce larger clutches (20–30) of smaller eggs (2 mm) and lack the specialized brilliantly colored tips on the elongate pelvic fins. The males of *Lestradea* and *Ectodus* possess different specific recognition signals, and their courtship behaviors differ from those of *Cunningtonia* and *Ophthalmochromis*. In *Lestradea* and *Ectodus* egg laying, fertilization, and collection by the female take place rapidly in that sequence. The courship behavior of *Asprotilapia* is unknown.

Members of the *Ophthalmotilapia* lineage occupy three types of habitat. Generally, *Asprotilapia*, *Cunningtonia*, and *Ophthalmotilapia* inhabit the offshore margins of the shallow, rocky littoral adjacent to the sandy bottom. *O. ventralis* often penetrates to greater depths of up to 5 m. *Lestradea* inhabits shallow areas with both sandy and rocky bottoms. *L. perspicax stappersi* is common at greater depths down to 50 m. The littoral habitat of *Ectodus* is much narrower, being confined to the shallow waters with sandy bottoms. Except for *Ectodus*, all members of the *Ophthalmotilapia* lineage are not restricted to a particular habitat but move freely between habitats with hard and soft bottoms. The absence of strong habitat restriction means the crossing of "alien" habitats whether or not conditions are adverse. As a result, a spectrum of food resources is exploited. Judging from the anatomy, stomach contents, and behavior in the laboratory, members of the *Ophthalmotilapia* lineage possess an extensive feeding repertoire. Thus the feeding pattern exhibited by the *Ophthalmotilapia* lineage resembles that of other cichlids in which increased functional and morphological differences in the trophic apparatus (dentition, jaw structure, skull morphology, and pharyngeal myology) do not necessarily lead to a greater separation on the food axis (Liem, 1980).

The comparative anatomical and phylogenetic data presented in this study reinforces the paradox (Liem, 1980; Greenwood, in prep.) that the morpho-

logically and phylogenetically most specialized cichlid taxa are not only remarkable specialists but also jacks-of-all-trades. How the morphological radiation of the feeding apparatus has evolved remains a major problem in understanding the causal factors underlying the spectacular diversifications in the cichlid trophic structures. If specialists are simultaneously jacks-of-all-trades, they defy the commonly accepted ecological notion that broadening the range of usable resources prevents species from specializing on individual types. So far, most studies have attempted to correlate the morphological diversity in the feeding apparatus of cichlids with adaptation and therefore fitness. However, Carson (1970) and Fryer (1977) have suggested that speciation and adaptation are not necessarily synchronous processes. Carson has offered evidence that in Hawaiian drosophilids speciation may have preceded adaptation.

Although there is no doubt that the *Ophthalmotilapia* lineage has undergone extensive morphological radiation in both skull structure and dentition, the data on morphology, function, trophic ecology, and behavior of this and other cichlid lineages (Liem, 1980) have failed to establish unequivocally that the morphological radiation is also adaptive.

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ABBREVIATIONS

a: anguloarticular
aap: adductor arcus palatini
ad: adductor branchialis
ad_5: fifth adductor
af: adductor fossa
am_1: adductor mandibulae pars A_1
am_2: adductor mandibulae pars A_2
am_3: adductor mandibulae pars A_3
ao: adductor operculi
ap: articular process
apa: ascending process of articular
apd: ascending process of dentary (coronoid)
appm: ascending process of premaxilla
apu: apophysis of upper pharyngeal jaw
bh: basihyal
boc: basioccipital
bs: basisphenoid
bsr: branchiostegal ray
ca: rostral cartilage
car: rostral cartilage
cb_1: first ceratobranchial
cb_5: fifth ceratobranchial (lower pharyngeal jaw)
cl: cleithrum
con: cranial condyle
d: dentary
do: dilatator operculi
e: ethmoid
eb: epibranchial
eb_1: first epibranchial
eb_{3-4}: third and fourth epibranchial
ect: ectopterygoid
ent: entopterygoid
eo: epiotic
eoc: exoccipital
ep: epaxial muscles
f: frontal
gha: geniohyoideus anterior
ghp: geniohyoideus posterior
hh: hyohyoideus
hhi: hyohyoideus inferior
hhs: hyohyoideus superior
hht: hyohyoideus transversus
hm: hyomandibula
hy: hyoid
ic: intercalar
im: intermandibularis
iop: interoperculum
la: lacrimal
l_1: palatomaxillary ligament

l_2: palatopalatine ligament
l_3: craniopalatine ligament
l_4: ethmopalatine ligament
lap: levator arcus palatini
le_4: fourth levator externus
li_{1-2}: first and second levator internus
lim: interoperculomandibular ligament
lo: levator operculi
lp: levator posterior
md: mandible
mml: medial mandibular ligament
mpt: metapterygoid
mx: maxilla
n: nasal
obp: obliquus posterior
od: obliquus dorsalis
op: operculum
p: palatine
pa: parietal
pb_2: second pharyngobranchial
pb_3: third pharyngobranchial
pb_4: fourth pharyngobranchial
pce: pharyngocleithralis externus
pci: pharyngocleithralis internus
pf: lateral ethmoid complex
ph: pharyngohyoideus
pm: premaxilla
pop: preoperculum
pp: postmaxillary process of maxilla
ppm: protractor pectoralis
ps: parasphenoid
pts: pterosphenoid
pv: vomer
q: quadrate
ra: retroarticular
rd: retractor dorsalis
rf: rostral fossa
sh: sternohyoideus
so: circumorbital
soc: supraoccipital
sop: suboperculum
sph: sphenotic
st: pterotic (supratemporal)
sy: symplectic
tda: transversus dorsalis anterior
tdp: transversus dorsalis posterior
tf: trigeminofacialis chamber
uh: urohyal
x: foramen of vagus nerve

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A Case History in Retrograde Evolution: The *Onca* Lineage in Anoline Lizards. II. Subdigital Fine Structure

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A CASE HISTORY IN RETROGRADE EVOLUTION: THE *ONCA* LINEAGE IN ANOLINE LIZARDS. II. SUBDIGITAL FINE STRUCTURE

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E. E. WILLIAMS[2]

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ABSTRACT. *Anolis annectens* is a presumed intermediate between the padless anole *A. onca* and more typical *Anolis* with adhesive toe pads. This study uses scanning electron microscopy to compare adult *A. annectens* with adult and juvenile *A. onca* and two species, *A. chrysolepis* and *A. auratus*, that were considered (Williams, 1974) to show stages in "retrograde" evolution of the anoline subdigital pad. Differences are found in scale shape, in scale contouring, and in the fine structural series. The fine structural series begins with short hook-like spines and terminates with setae which have a long stalk and a triangular tip. In generalized anoles, setae cover the surface of the expanded lamellar scales which form the pad. The spines appear to function as prehensile devices, while the setae may combine prehensile and adhesive mechanisms. *A. auratus* parallels *A. annectens* in showing dedifferentiation of the pad (reduction in pad width, in lamellar number, and in the distinctness of the pad from the phalanx i region), but the distribution of setae is expanded in *A. auratus*, not restricted as in *A. annectens*. The subdigital specializations of *A. auratus* may reflect adaptation to the complex surface architecture of grass blades and stems. *A. annectens* and *A. onca* appear to be on a very different adaptive pathway. Short spines partly or completely replace setae, and the lamellar scales are partially or completely replaced by multicarinate scales. Comparative data from a variety of anoles, non-anole iguanids, and geckos suggest that the subdigital specializations of *A. annectens* and *A. onca* may be correlated with radiation into sandy substrates and thorn scrub vegetation. The absence of definite keels in juvenile *onca*, in contrast to

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their extreme development in adult *A. onca*, is believed to be an ontogenetic adaptation which coincidentally parallels the phyletic sequence. *A. chrysolepis*, with somewhat narrowed pads and a few subdigital keels, is a suitable structural ancestor for *A. auratus* as well as *A. annectens* and *A. onca*.

The alternative adaptive pathways leading to *A. auratus* and *A. onca* emphasize that "retrograde" is purely a descriptive term calling attention to the dedifferentiation of a typical *Anolis* digital pad, *not* a statement of loss of adaptive value for the end points in the "retrograde" series.

INTRODUCTION

In an earlier paper one of us (Williams, 1974) described a new species, *Anolis annectens*, whose subdigital morphology represented an intermediate between the adhesive toe pad of generalized anoles and the keeled subdigital scales of *A.* (*Tropidodactylus*) *onca*. On this basis and other comparative data, the earlier paper: 1) proposed a series of morphological stages in the loss of the subdigital adhesive pad, 2) suggested that *A. annectens* was derived from an *A. chrysolepis* "stage" of the mainland beta anoles and represented an intermediate stage in the evolution of the very specialized condition in *onca*, and 3) discussed probable correlations of habitat and subdigital morphology.

In this paper we amplify and examine these ideas, drawing upon new and more detailed morphological data obtained by scanning electron microscopy (SEM) from *A. annectens*, *A. onca*, their probable relatives, and still other species that appear to provide insight into the morphological sequence of pad loss.

MATERIALS AND METHODS

The size, sex, and source for specimens used in the study are given in Table 1.

In the previous paper the fourth toe of the hindfoot formed the basis for interspecific comparisons (Williams, 1974). Because *Anolis annectens* is known only from the unique type, we have shifted our attention to a toe not described or figured in the original paper. All descriptions of fine structure in *annectens* and other species are based on the third toe of the hindfoot. However, except in *annectens*, we have also examined the fourth toe of each species.

Phalangeal dimensions were taken

Table 1. Specimens examined.

		Snout-vent length (SVL)
Anolis annectens	*holotype FMNH 5679	68.5 mm male
Anolis onca	*MCZ 158248	67 mm male
	MCZ 158249	83 mm male
	MCZ 158250	77 mm female
	*MCZ 158251	69 mm male
	*MCZ 154068	26 mm (juvenile)
	MCZ 154067	25 mm (juvenile)
Anolis chrysolepis	*LACM 74485	62 mm male
	MCZ 43856	62.5 mm male
Anolis auratus	*LACM 72781	54 mm female
	MCZ 77428	47.5 mm female

* Measurements and illustrations are largely based on these animals.
Abbreviations:

FMNH	Field Museum of Natural History, Chicago, Illinois
LACM	Los Angeles County Museum of Natural History, Los Angeles, California
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts

with dial calipers or an ocular micrometer. In discussing the subdigital scales we number them from claw to palm. Phalangeal number is counted in the same fashion from distal to proximal.[1]

Specimens were prepared for microscopy by cutting the third and fourth toes from the foot at the metatarsal-phalangeal joint. The toes were then critical-point dried and coated with carbon followed by gold/palladium. Coatings were applied in 15–20 sec. bursts to avoid the possibility of heat damage.

Measurements of fine structure were made from photographs corrected for the magnification given by the instrument. Manufacturer's specifications suggest that the error in reported magnification may be as high as 20%, although with some care it is unlikely to be more than 10%. The *annectens* specimen was photographed twice, with eight weeks separating the sessions. Measurements of seta and scale dimensions taken from the two sets of photographs differed by 3–8%. Where photographs were taken at an undetermined angle to the plane of the structure, an angular correction is estimated, and the data are reported as approximate. More precise measures are reported as the mean of 6–20 individual measures along with the 95% confidence limit of the mean.

ANOLIS ANNECTENS MORPHOLOGY

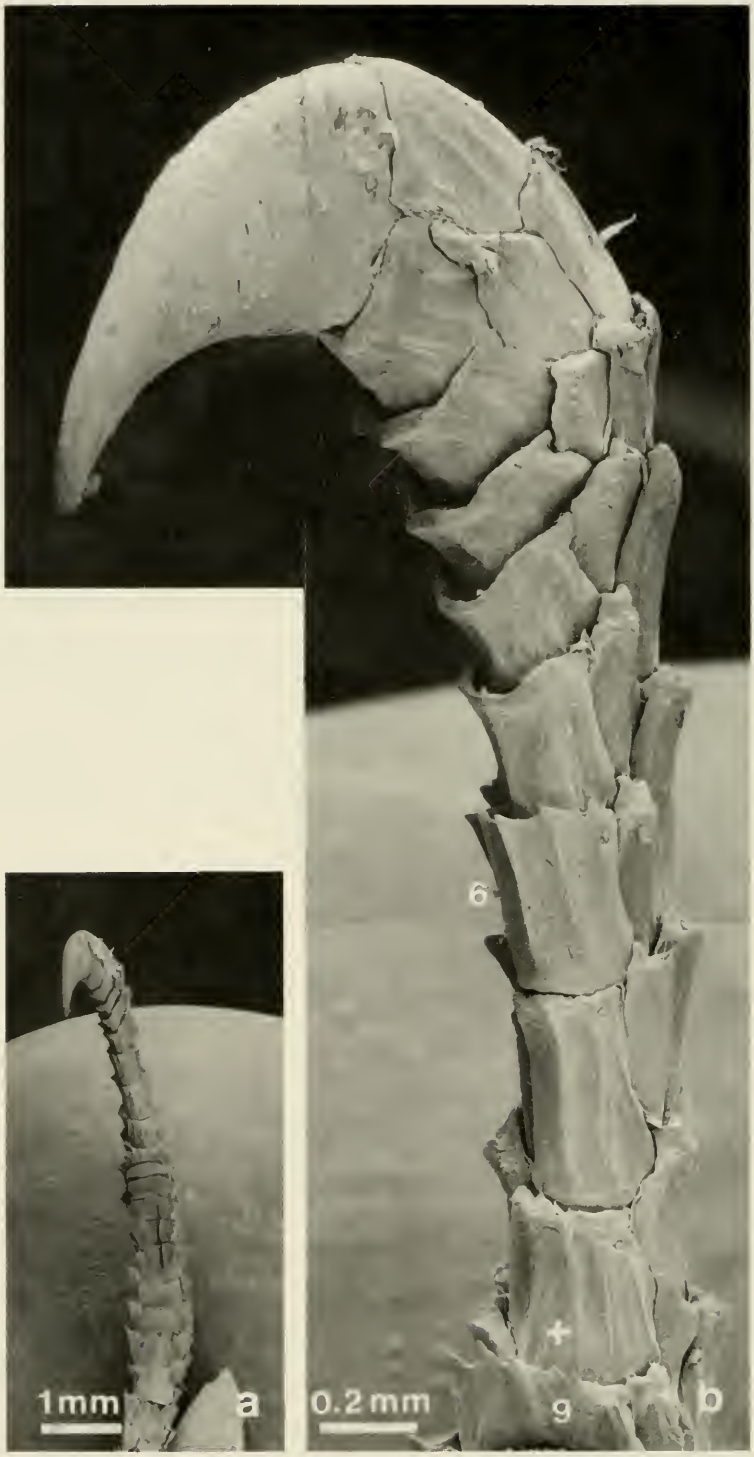
There are 20 subdigital scales on the third toe: one over the claw base, seven under phalanx i (2–8), six under phalanx ii (9–14), and six under phalanx iii (15–20) (Fig. 1). The subdigital scales fall into three morphological groups: a) multicarinate scales, b) lamellar or lamellar-like scales, and c) unique scales of an intermediate type.

a) Scales 1–8 (i.e., all those distal to phalanx ii) and 16–19 are multicarinate (scale 20 was cut at the palm, but presumably belongs in this group). These are relatively narrow, have robust, unfrayed distal margins studded with "mechanoreceptors" (see Schmidt, 1920; Miller and Kasahara, 1967; Hiller, 1968), and closely resemble the scales on the lateral margins of the toe.

A typical multicarinate scale has three to five keels. The keels originate near the proximal base of the scale and expand distally into large rounded bosses. The crests of the keels are bare and devoid of surface structure apart from a few striations (Fig. 3). The striations are probably produced by wear. Mechanoreceptors are usually positioned just distal and in the lee of the keels.

The keels throw the surface of the scale into sharp relief. The slopes of the keels are covered with spines (for terminology of spine to seta series see Fig. 21). Although there are intermediate sizes and variation in spine size is actually continuous, two major size classes of spines can be distinguished. The larger, more numerous spines are 0.9–1.2 μ tall and 0.5–0.75 μ in diameter near their base (Fig. 3). They occur in a density of 1.75 spines/sq μ. These are interspersed with nubbin-like small spines (0.1–0.5 μ tall; 0.2–0.3 μ in diameter near the base). The shape of the spine tip varies from sharply recurved to almost straight. Recurved spines with the tip pointing distally and toward the crest of the keel are the most common. The spine bases are formed by buttresses or struts (Ruibal, 1968), so that the scale surface appears to be pinched or pulled up into spines. The centers of the spines are 0.6–0.8 μ apart, and regions like that shown in Fig. 3c have a density of 2.0 spines/sq μ. The spines are separated

[1] Numbering the phalanges from distal to proximal and ignoring the claw has been the convention in taxonomic descriptions of *Anolis* since at least Boulenger (1885). It has therefore been used here, as it was in Williams (1974). Morphologists, since they emphasize the number of phalanges in each digit, have preferred to count from proximal to distal (e.g., Russell, 1975). We have preferred consistency within this series and within taxonomic literature to congruence with the morphological literature. The discrepancy is radical, but in each case context should make the usage clear.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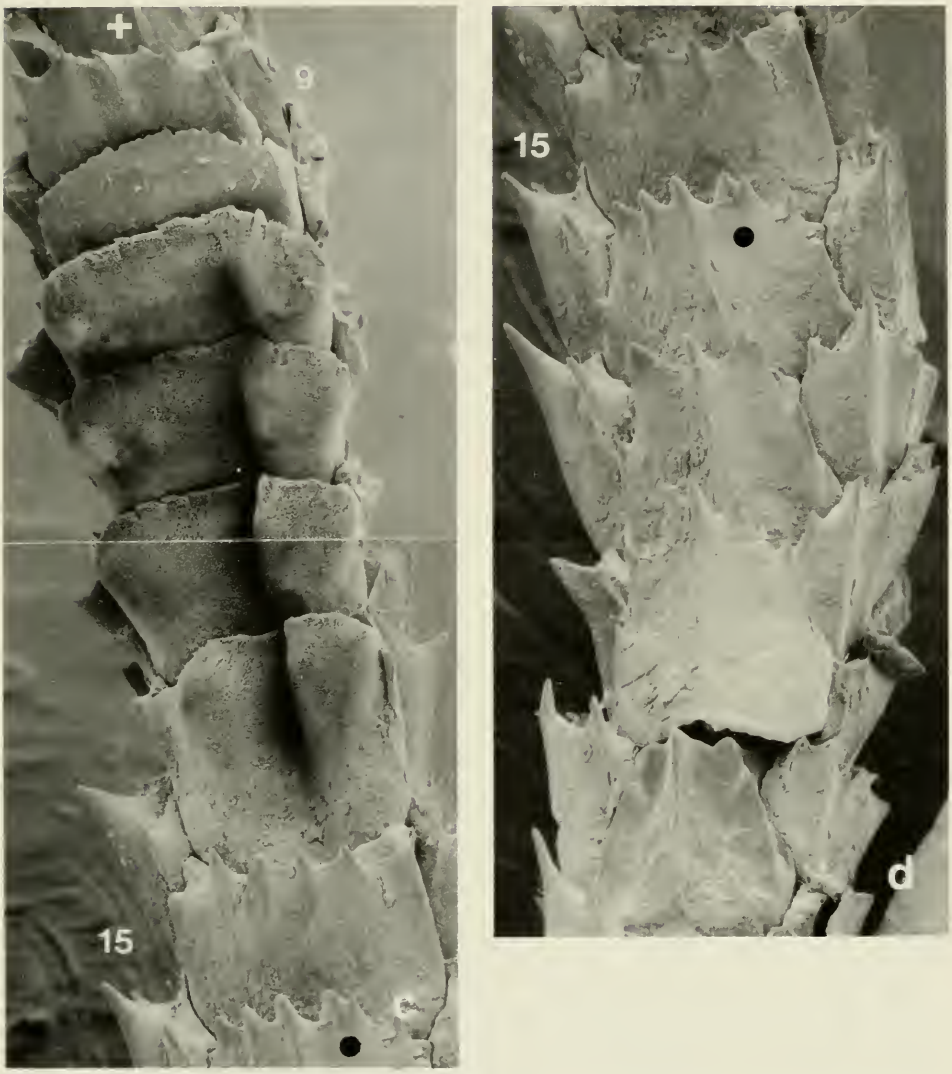


Figure 1. The third toe of *A. annectens*. a) Shows an overall view. Phalanx i(b), ii(c), and iii(d) scales are shown as montages; (b) and (c) match at "+" and scale 9; (c) and (d) match at the "●" and scale 15. Scales are numbered from the claw.

into irregularly shaped fields by narrow (0.6 μ) "trackways." The trackways presumably represent the borders of the epidermal cells (Ruibal, 1968).

The general pattern described above is modified slightly in the proximal portion of the scales of phalanx iii. In these regions the scale surface is slightly contoured into low "hillocks" (Figs. 1, 3) which appear to correspond to a single epidermal cell as each is completely bounded by a trackway (see also Figs. 6 and 7 of adult *A. onca*). The density of spines increases slightly between the trackway boundary and the crest of the hillock. This variation also occurs on the lateral digital scales.

b) Subdigital scales 10–14 resemble la-

Figure 2. Oblique view of the phalanx ii scales of the third toe in *A. annectens*. The keels and bosses on the lamellae and intermediate scales are indicated by small arrows. Note the relief of the keels and bosses on scales 9, 14, and 15. The arrow adjacent to the dimensional scale indicates the direction of the claw (distal). This convention is used in subsequent figures.

mellae in having a distinct, thin, frayed free margin and in being laterally expanded to form a pad.[1] They differ from typical *Anolis* lamellae in having small bosses or keels along their lateral margins (Fig. 2). The surface architecture of the bosses is similar to that of the keels on the multicarinate scales.

The central portion of each of the lamellar scales is covered with setae (Fig. 4). The setae are about 20 μ tall (shorter near the base of the scale and margins), have a terminal "spatula," and occur with a spacing of about 1 μ (density of 1–2 setae/sq μ). Midway between the spatula and the scale surface, the shaft of the seta is round in cross section and 0.48 ± 0.08 μ in diameter. The shaft tapers slightly (to 0.35–0.45 μ in diameter) toward the spatula. At about 1.4 μ proximal to the spatula the setae are usually inflected slightly toward the claw and the shaft becomes oval in cross section (dimensions are about 0.25–0.35 μ by 0.2 μ). Just proximal to the spatula the shaft is constricted and bent toward the metatarsal-phalangeal joint. The two inflections in the shaft are responsible for orienting the spatula so that its free distal margin faces the metatarsal-phalangeal joint, and its expanse is 30°–90° from the vertical plane of the shaft (orientation varies significantly). The distal margin of the spatula is usually frayed, and it may be concave toward the lamellar surface. The spatula itself is shaped like an isosceles triangle with a base of 0.73 ± 0.09 μ and a height of 0.58 ± 0.02 μ. The area of the spatula is 0.211 ± 0.022 sq μ. The morphology of the setae in *annectens* is very similar to that in generalized anoles (e.g., *A. carolinensis* and *A. sagrei* as described by Ruibal and Ernst, 1965).

c) Subdigital scales 9 and 15 (Figs. 2, 5) exhibit a blend of lamellar and multicarinate scale features.

Scale 9 is laterally expanded, but less so than the more proximal lamellar scales. Unlike the lamellae, the distal margin is quite robust, and there are eight small bosses or keels along the distal margin. One of these shelters a me-

[1] The outer keratin layer was absent on scale 10, but there are some probable "boss" sites and a relatively thin margin. We have included it with the lamellar-like scales on the basis of these characters.

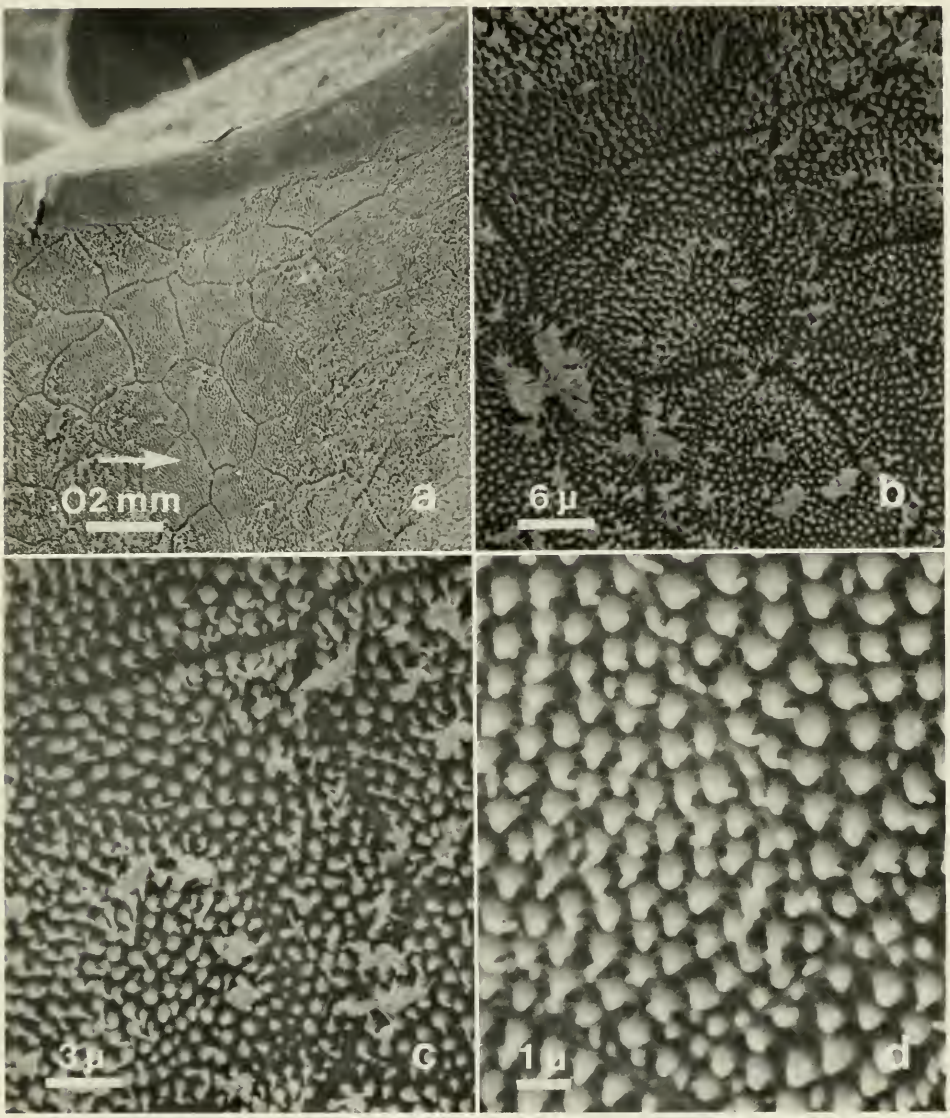


Figure 3. The fine structure of multicarinate scale 17 in *A. annectens*. a) Shows the central keel and adjacent fields of spines. b), c), and d) Are progressively higher magnifications of the spinate surface. Note the low hillocks in (b) and (c) and the presence of many small spines and knobs in (d) (compare with Figs. 21 and 22).

chanoreceptor. The surface of the scale appears "velvety," but less so than the lamellar scales. Based on gross characters it is neither a lamellar nor a multicarinate scale.

The fine structure also suggests the intermediate character of the scale (Fig. 5; Fig. 21 for definition of types). The surface architecture of the bosses is similar to that of the keels on the multicarinate scales. In a few regions, particularly adjacent to the central keels, there are fields of small spines (0.2–0.3 μ diameter at the base; a density of 2.2 spines/sq μ).

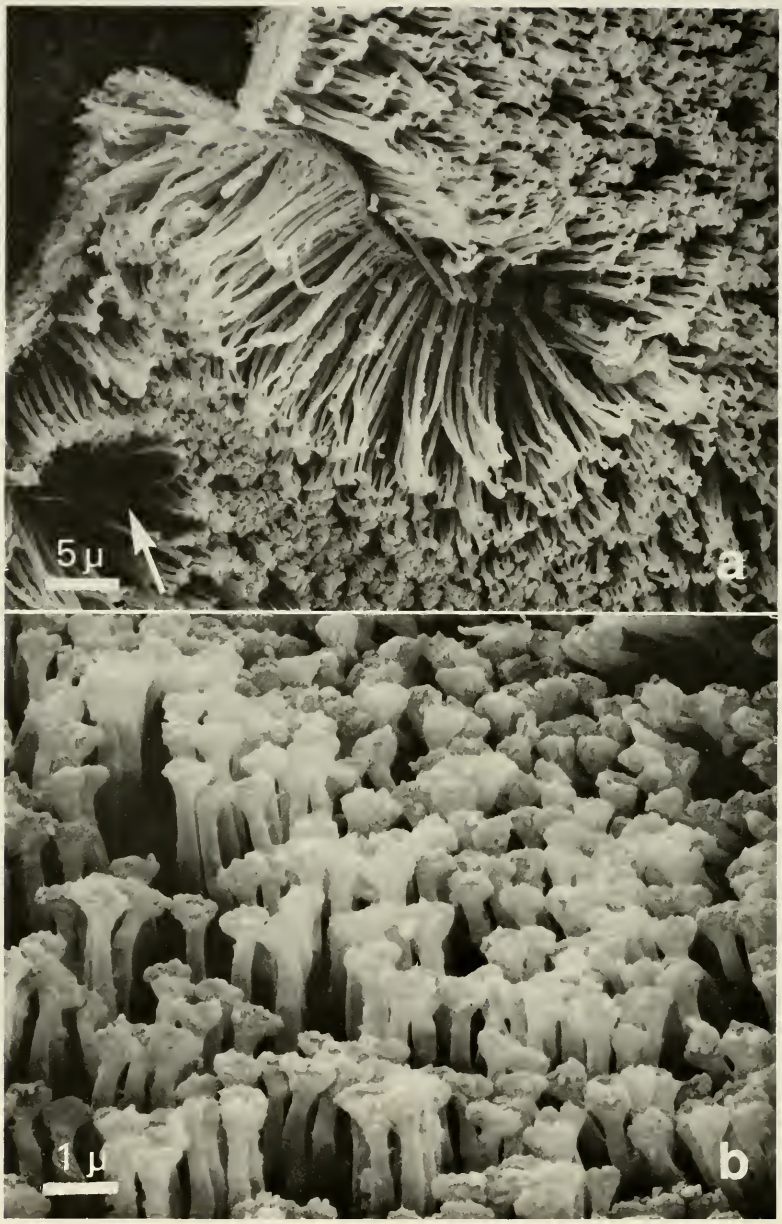


Figure 4. The setae on scale 12 (lamella 3) in *A. annectens*. a) Shows setae along the distal margin of the lamella. b) Is a view of the spatulae as seen from the claw.

These are taller, but otherwise similar to the small spines on the multicarinate scales. The zones of small spines are bounded by regions of somewhat larger spines (Fig. 5b and lower left and center top of Fig. 5c). These spines have the diameter (0.55 μ at the base) and spacing characteristics of the larger spines on the

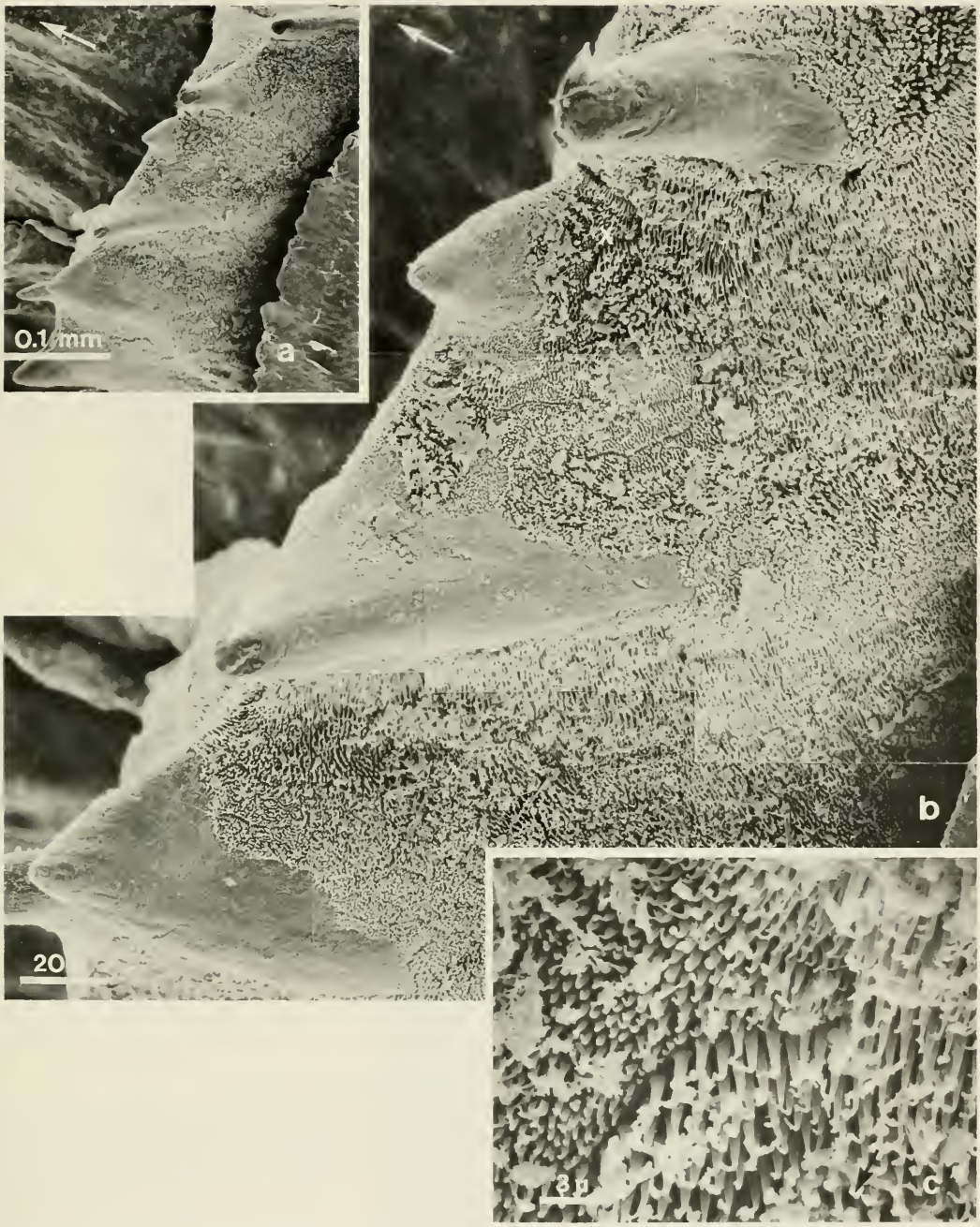


Figure 5. The morphology of scale 9 in *A. annectens*. a) Shows an overall view. b) A montage of half the scale surface illustrates the heterogenous fine structure and relationship of the keels and spine/spike/seta series. The region indicated with an "x" is shown in higher magnification in (c). Note the spines to the left of (c), the abrupt transition from spines to prongs along the bottom of (c), and the gradual transition from spines to spikes to prongs along the top of (c). A few seta shapes occur to the lower right (black arrow).

multicarinate scales, but grade up to 5 μ in height (by definition; see below). Most of the scale, however, is covered by even taller, more robust "spine-like" forms which grade through a variety of shapes into a few setae. The much taller (above 5 μ) and thicker (0.7–0.8 μ at the base; 0.5 μ midpoint diameter) structures with strongly tapered, needle-like tips we refer to as spikes (Fig. 5 center top; Figs. 21, 22). The gradation from spines to spikes may be abrupt, as along the center of Fig. 5c, or very gradual, as along the top of Fig. 5c. The spikes in the lower and right portions of the figure are interspersed with structures, here called "prongs," which have a straight or recurved tip which is less tapered than the spike (see also Figs. 21, 22). There are seta shapes (defined by the expanded triangular tip) in the lower left of the figure (note black arrow; see also Fig. 21). Setae are rare compared to spikes and prongs. In just a few areas adjacent to the "bosses" and over the central portion of the scale, spikes and prongs grade into setae. The dimensions of the spatula on these setae are comparable to those of spatulae on the lamellar scales, and the midpoint diameter of the stalk is also similar. Setae on scale 9 differ only in their shorter stalk (6–7 μ compared to about 20 μ for the lamellar setae). Although we have not encountered setae this short elsewhere, height is probably not a reasonable basis for differentiating them from the setae on the lamellar scales because 1) a few of the setae from the marginal and proximal areas of the lamellar scales are almost this short (about 10 μ), and 2) stalk height is a variable character within and between anole individuals and species (Peterson and Williams, unpublished data).

Scale 15 is quite similar to scale 9, although there are more definite keels along its lateral margins (Figs. 1, 2). These are almost certainly serially homologous with those on multicarinate scale 16 and lamellar scale 14. The adjacent multicarinate scales have a dominant central keel which is missing on scale 15. The fine structure of scale 15 was difficult to examine thoroughly because of the debris on its surface. There are spines grading into spikes, as on scale 9, but we were unable to confirm that setae are present. Scales 9 and probably 15 combine the features of lamellar and multicarinate scales and suggest a model for evolutionary intermediate morphology.

COMPARISON WITH *ANOLIS (TROPIDODACTYLUS) ONCA*

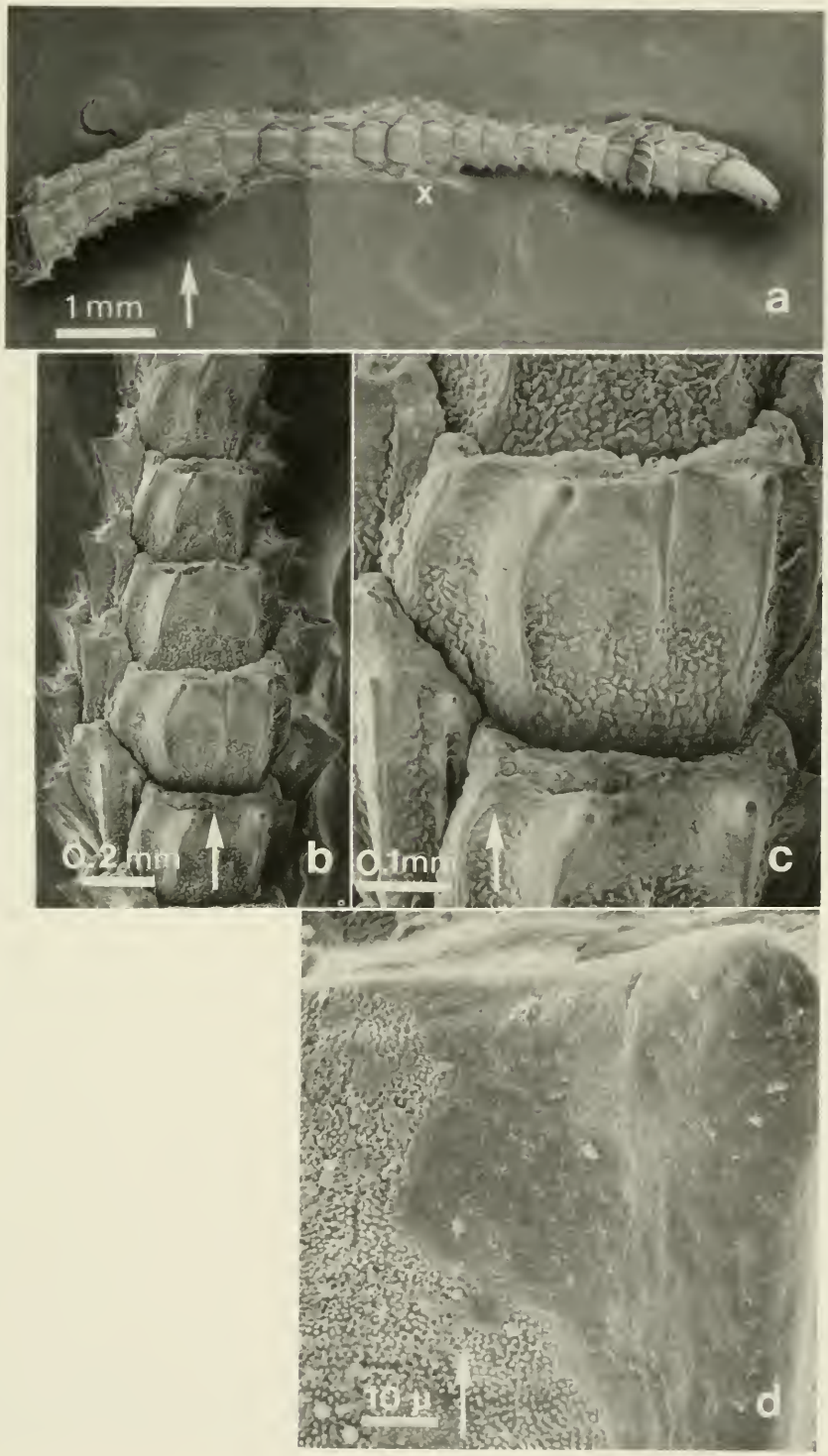
Adult Morphology

There are more subdigital scales in *A. onca* than in *A. annectens* (24 rather than 20, Figs. 1, 6). This reflects a) the longer phalanges in an *onca* of approximately the same snout-vent length as the *annectens* type (phalanges ii and iii are 2.3 mm and 2.8 mm compared to 1.4 mm and 2.4 mm, respectively, in *annectens*), and b) differences in the size of the scales in some regions. The distribution of scales relative to the phalanges in *onca* versus *annectens* is: 1/1 claw base; 9/7 phalanx i; 6/6 phalanx ii; and 8/6 phalanx iii. In *onca* the scales under phalanx ii are longer, and those under phalanx iii are shorter than in *annectens*.

While there is some regional variation in the morphology of the subdigital scales, all of them are multicarinate (Fig. 6). Four or five robust keels are present,

→

Figure 6. The third toe of *A. onca*. a) Only the distal 22 scales are shown. The "x" indicates the scale shown in (b) center. b) Shows multicarinate scales 8, 9, 10, 11, and 12 at the i/ii interphalangeal joint. Note the more prominent median keel on scale 11, the asymmetry of the keels, and the great relief of the keels on the lateral digital scales. c) Shows the structure of an individual scale. Hillocks occur toward the base of the scale, and the two pairs of lateral keels are most prominent. d) Illustrates the bare surface of the keel and junction with adjacent spinate areas. Note the "wear striations" along the crest and proximal slopes of the keel.


x
1 mm
a
0.2 mm
b
0.1mm
c
10 μ
d

and the distal margins of the scales have additional bosses. The distal margin is definitely not thin or frayed, and numerous mechanoreceptors occur in the lee of the keels and bosses. The regions between the keels and toward the base of the scale are somewhat velvety in appearance and heavily contoured into hillocks (Figs. 6, 7). The subdigital and lateral scales have very similar gross morphology.

All the subdigital scales in *onca* resemble the multicarinate series (scales 1–8, 16–20) in *annectens*. There is a difference, however, in the prominence and placement of the keels. The pattern in both animals is based on five possible keels: a median keel, a pair of lateral keels, and a pair of far lateral keels. In *onca* the four lateral keels are consistently well developed with the lateral pair being the most robust and prominent, while the fifth or median keel is conspicuous only adjacent to the interphalangeal and metatarsal-phalangeal joints (Fig. 6). This differs from the condition in *annectens* in which the median keel is always well developed and the most prominent of the five keels.

The fine structure of the keels in *onca* appears similar in every respect to that of the keels in *annectens* (Fig. 6).

The areas between the keels are covered with spines. Distally on the scale where hillock contouring is not well developed, the spines are relatively uniform (Fig. 7c). They are 0.8–1.2 μ tall and 0.3–0.45 μ in diameter near the base (0.1–0.2 μ in diameter at their midpoint) and occur in a density of about 1.2 spines/sq μ. The tips are sharp and recurved, usually toward the crest of the keel.

Most of the scale surface, however, is heavily contoured, and in these areas the spines are more varied in morphology and spacing (Fig. 7d). The range of spine height becomes 1.0–1.8 μ, and there is marked variation in robustness. While some spines resemble those near the distal margin, others have extremely large buttresses or struts, so that their diameter at the base (0.8 μ) is as much as half their height. Spacing between the center of the spines ranges from 0.7 μ near the crests of the hillocks where the buttresses of adjacent spines interdigitate to more than 3 μ in the depths of the valleys between the crests.

The spinose regions of the scale in *onca* differ from those in *annectens* only in a) the scarcity of small spines (these are present, but rare), and b) the more extreme development of contouring and associated spine variation.

Juvenile Morphology

Juvenile *onca* have a different subdigital morphology from that of the adults (Maderson and Williams, 1978). The number (24) and distribution of the subdigital scales relative to the phalanges do agree with the condition in the adults. But, in contrast to the adults, none of the scales are strictly multicarinate (Fig. 8a). There are two poorly differentiated series: a) scales in the phalanx ii and iii regions (scales 10–24) and the distal and proximal scales in the phalanx i region (scales 1, 8, 9), which have less robust ridges near the distal margin and a more velvety appearance (Fig. 8b), and b) scales in the mid-phalanx i region (scales 2–7), which have more robust ridges and a less velvety texture (Fig. 9a).

a) Scales 8–24 have a narrow but lamellar-like shape particularly because they flare distally, but they lack the frayed distal margin which is characteristic of lamellae (Fig. 8b, 8c). In most cases the scales are proportionally wider than in the adult, but the difference is often very small. Instead, the major differences between hatchling and adult morphology are in the more velvety appearance and the absence of robust keels with sharp crests and "bare areas" (compare scale 13 shown in Fig. 8b with scale 11 shown in the lower portion of Figs.

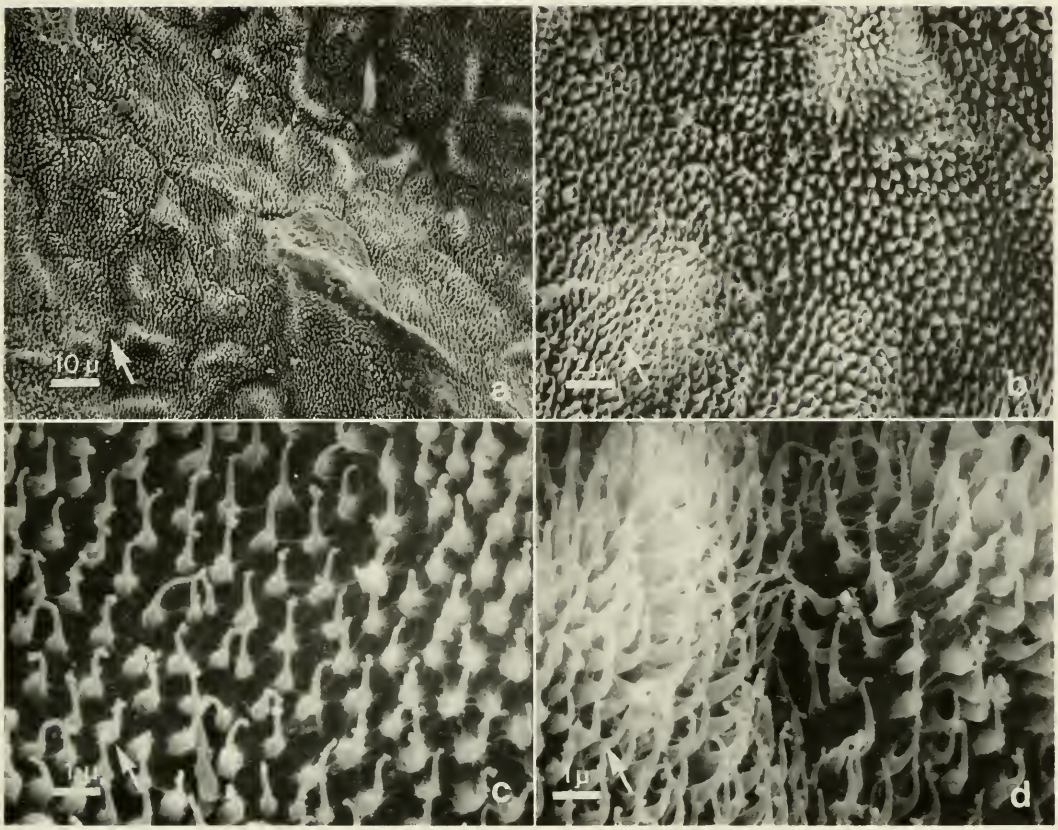


Figure 7. The third toe of *A. onca*. a) Shows detail of the surface of scale 7. A small keel occurs in the lower right. b) Shows detail of the hillocks. c) Is taken on scale 7; d) is from scale 11. c) and d) Illustrate the differences in spine morphology between countoured and uncountoured regions.

6b and 6c). In the hatchling, the surface of the scales is gently contoured into ridges which occur in positions corresponding to the robust lateral and far lateral keels of the adult. There is, however, no ridge that anticipates the median keel. Mechanoreceptors often occur in the lee of the lateral contours, and the scale bases are also contoured into low hillocks.

Setae are not present on any of the third or fourth toe scales. The distal half or two-thirds of the scale surface, including the contoured ridges, is covered with spikes and prongs (for definitions see Figs. 21, 22). Shorter spikes at the margin itself grade into taller spikes proximal to the margin (7.2 ± 0.51 μ tall; 0.56 ± 0.08 μ in diameter). In some areas the spikes grade into forms with a more robust prong-like tip (in Fig. 8d spikes in the upper left are shown grading into prongs in the lower right). Between the contoured ridges as well as proximally, the scale surface is covered with spines (Fig. 9b). There is continuous variation in spine height from about 0.75 μ up to the spike morphology at 5 μ.

Although its shape is quite different, scale 1 is included in this series because its contouring and fine structure are comparable to those of scales 8–24. The surface of the scale is covered with spikes and prongs 5–7 μ tall.

b) Scales 2–7 in the juvenile have a

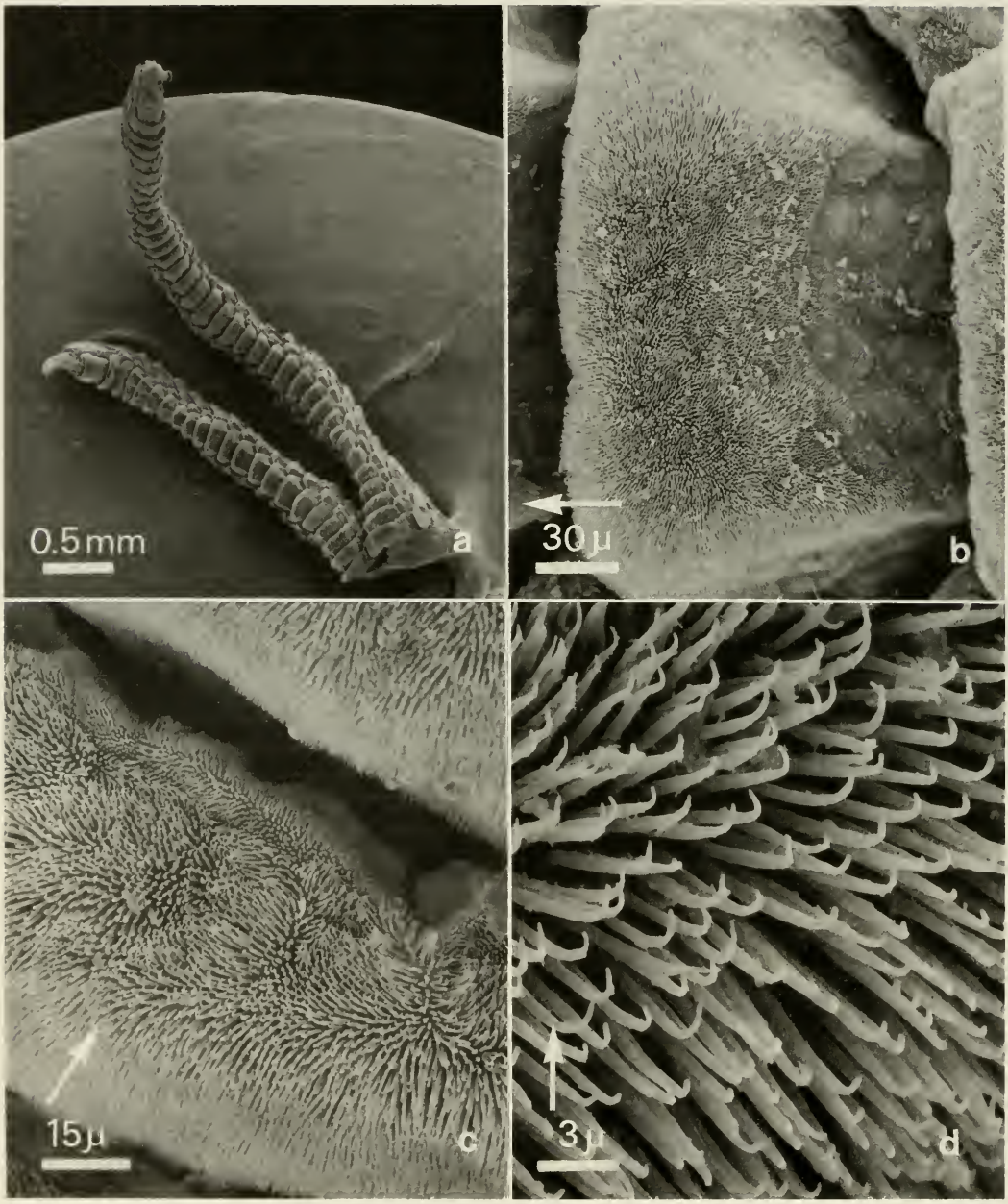


Figure 8. The third and fourth toes of juvenile *A. onca*. a) Shows an overall view. b) Shows scale 13; the lamellar-like scales in the phalanx ii region of the third toe have contours in the position of the lateral keels. c) Shows a robust distal scale margin. d) The surface of the scale is covered with spikes (upper left portion) and prongs (lower right portion).

gross shape similar to their homologues in the adult, and the position of the ridges in most cases anticipates the position of keels in the adult.

The scale surface adjacent to the distal margin and that over the distal portion of the ridges is covered with spines (Fig. 9a). On scale 6, spines in the distal region

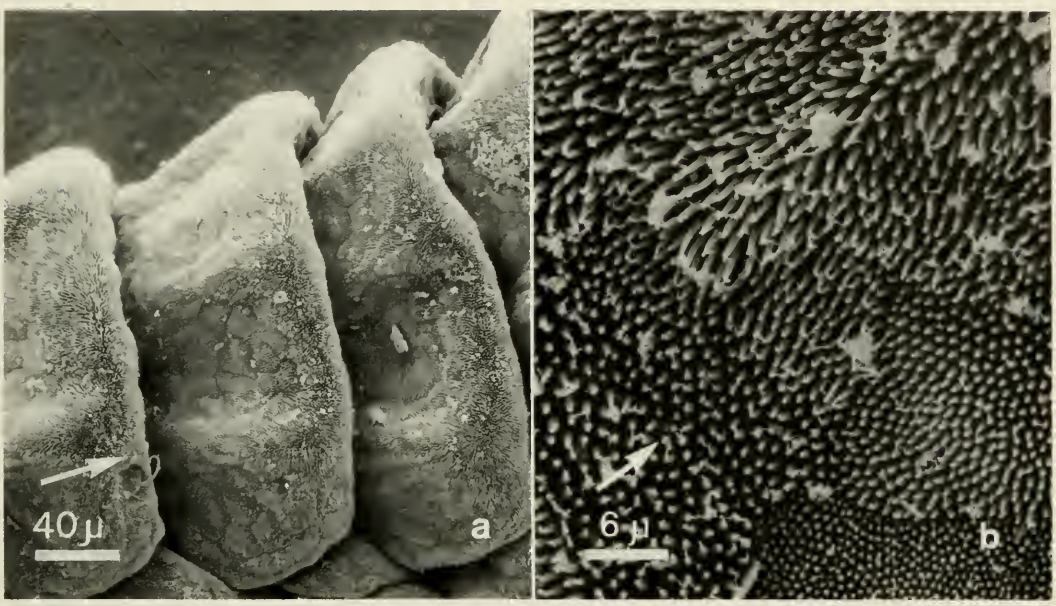


Figure 9. The second, third, fourth, and fifth scales of the third toe (phalanx i region) of juvenile *A. onca*. a) Shows 3–4 μ tall spines along the distal margin and over the ridges. The region between the contours and toward the base of the scale is covered with shorter spines. b) Illustrates the border between the distal and proximal spines on scale 5.

are 3.37 ± 0.75 μ tall and 0.47 ± 0.08 μ in diameter (see the top portion of Fig. 9b). These grade more or less abruptly into spines which are more comparable to those of the adult (1–2 μ tall; 0.5 μ diameter at the base; and a range of densities of 0.7–1.2 spines/sq μ; see the lower portion of Fig. 9b). In some proximal areas fields of still smaller spines occur (0.5 μ tall; 0.3 μ diameter at the base; and 2 spines/sq μ; see the lower right corner of Fig. 9b).

Scales 7 and 8 at the boundary between the series are not very different in shape, contouring, or fine structure. The "spines" on scale 7 are 4–5 μ tall, while the spikes on scale 8 are 6–7 μ tall. The subdigital scales are regionally differentiated more than in the adult, but much less than in *annectens* or *chrysolepis*.

Some of the lateral digital scales have robust keels with bare areas, but most of the scales immediately adjacent to the subdigital series have ridges (Fig. 9a) rather than keels as in the adult (Fig. 7b).

COMPARISON WITH *ANOLIS CHRYSOLEPIS*

A. chrysolepis has 29 subdigital scales (a second specimen has 27; Fig. 10). The distribution of these scales relative to the phalanges in *chrysolepis* versus *annectens* is: 1/1 claw base; 10/7 phalanx i; 11/6 phalanx ii (9/6 in the second specimen); and 7/6 phalanx iii. The differences in distribution reflect smaller scales over phalanges ii and iii in *chrysolepis* and a longer second phalanx in *chrysolepis* (2.1 mm compared to 1.4 mm in *annectens*; phalanx iii is 2.3 mm in *chrysolepis* and 2.4 mm in *annectens*).

The subdigital scales of *chrysolepis* include a) lamellae (scales 13–22), b) generalized subdigital scales which are defined as non-lamellar and unkeeled (scales 10–12, 22–29), and c) scales with small keels or boss-like areas (scales 1–9; Fig. 12).

a) The lamellar scales lie under phalanx ii, form a pad, and resemble the la-

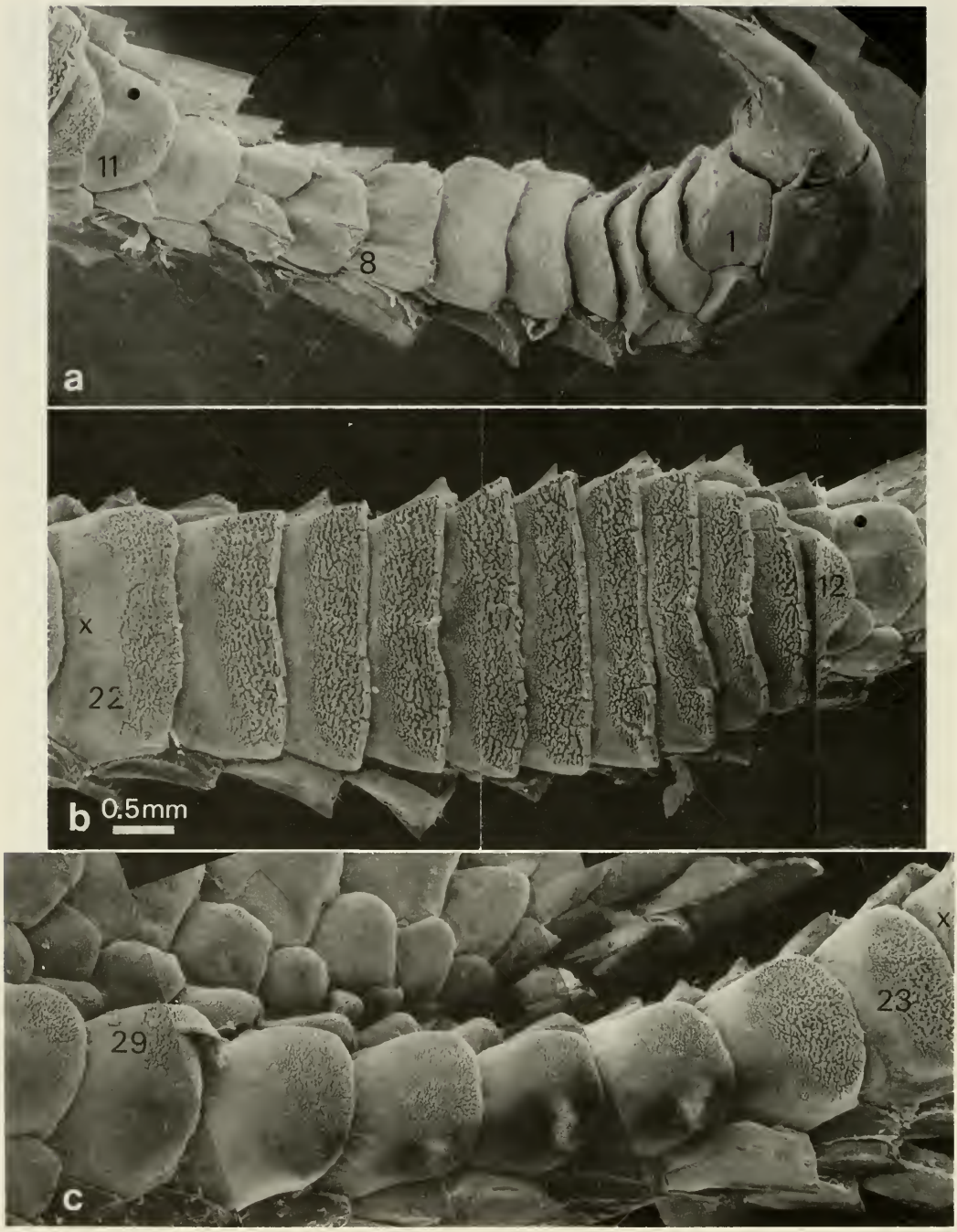


Figure 10. Composite of the third toe in *A. chrysolepis*. The distal scale series (a) fits with the pad series (b) at the "●"; the proximal series (c) matches (b) at "x."

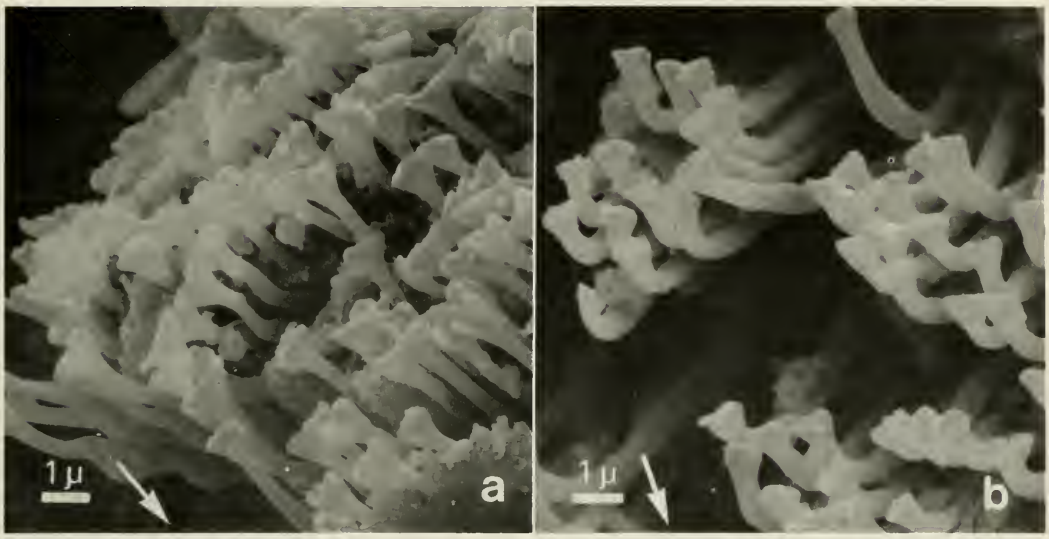


Figure 11. The setae in *A. chrysolepis*. a) Is taken on the eighth lamellae (scale 20) adjacent to the distal margin (the material below the spatulae is debris). b) Is taken on scale 28 just distal to the metatarsal-phalangeal joint. The setae on scales 28 and 30 are slightly narrower than on the lamellar scales (0.84 ± 0.05 μ compared to 1.01 ± 0.07 μ; the height of the spatula is not different), and the stalk is less tapered and thicker just below the spatula. The difference in density of setae is an artefact of the sites chosen.

mellae of generalized anoles. There is no evidence of small keels or bosses like those of *annectens*. The surface of these scales is covered with setae (Fig. 11). The orientation and height of the setae are comparable to those of *annectens*, but the stalk diameter (0.79 ± 0.09 μ at the midpoint) and spatular dimensions (base [width] 1.01 ± 0.07 μ; height [length] 0.71 ± 0.05 μ; area 0.358 ± 0.037 sq μ) are larger. The *chrysolepis* measurements are unusually large for *Anolis*. The dimensions in *annectens* are similar to those of West Indian anoles investigated by us and by Ruibal and Ernst (1965).

b) Proximal and distal to the lamellae there are unspecialized subdigital scales (Figs. 10, 12). These have a fairly robust rounded distal margin and a velvety surface texture. Mechanoreceptors occasionally occur along their distal margins. The shape of these scales is highly variable. The series of scales proximal to the pad continues beyond the metatarsal-phalangeal joint and into the sole of the foot. Scales with these gross characters occur proximal and distal to the pad in most anoles we have examined.

There is a poor correlation between this gross morphology and the fine structure of the scale. In *chrysolepis* the scale series proximal to the pad (scales 23–29 and beyond into the sole of the foot) bears setae with well-defined spatulate tips (Fig. 11). Distal to the lamellae only one of the scales with this gross morphology bears setae. This is scale 12, which is adjacent to the lamellae and part of the raised pad. Scale 11, distal to the pad, bears tall spikes with tips which combine the shape characters of the seta and the prong (Fig. 13). The tip is flattened or compressed like the spatula, but not laterally expanded to form a triangular surface and broad distal margin (in generalized anoles this unexpanded tip shape is present in the very proximal portion of the lamella as part of the morphological grade from spines to setae; Fig. 23). The seta/prong intermediate morphology occurs over the central portion of scale 11 (the distribution is evi-

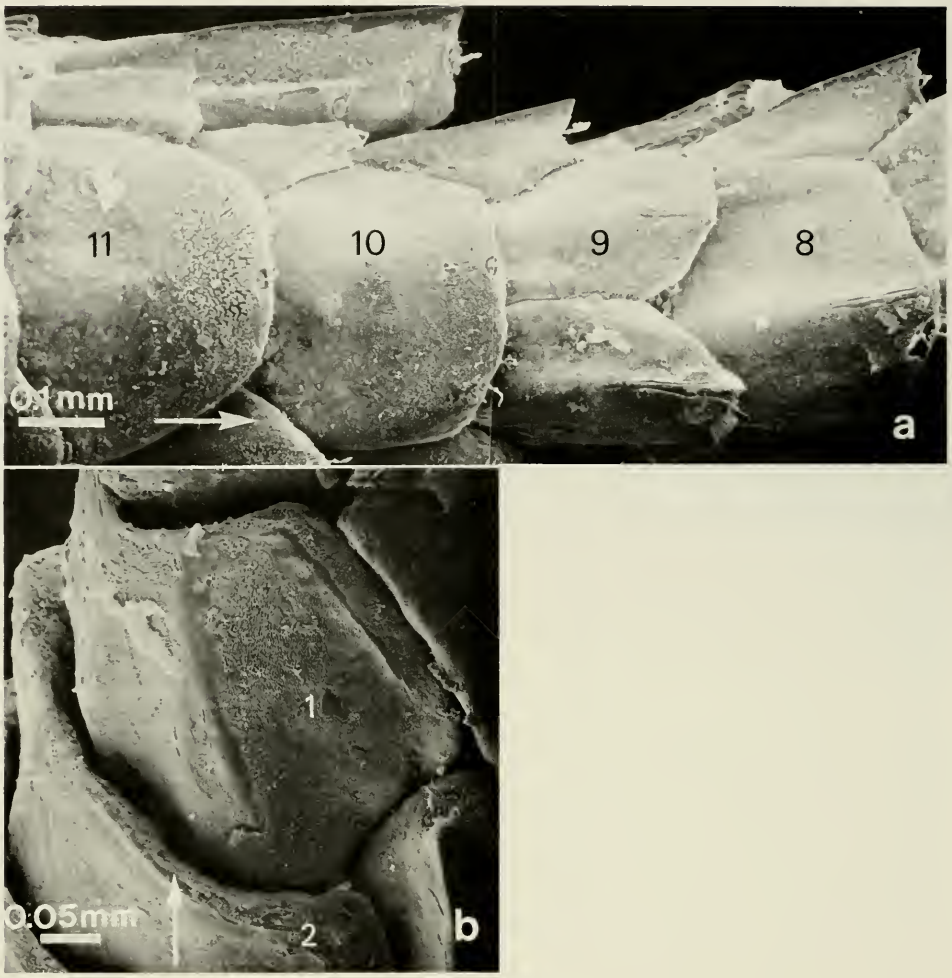


Figure 12. Scales distal to the pad in *A. chrysolepis.* a) Shows the scales just distal to the pad. b) Is an oblique view of scales 1 and 2. Ridges (scale 1), small keels (e.g., scale 8), or bare areas (e.g., scale 2) are present on the series 1–9.

dent from Fig. 13a). Toward the lateral and proximal portions of the scale the shape grades into a blunt prong and finally a short spine with a recurved tip. The spinose regions of the scale exhibit contouring similar to that seen in *annectens.*

c) The still more distal groups of scales (scales 1–9) grossly resemble scales 10 and 11 with the addition of small keels or keel-like bare areas (Figs. 12, 14). The fine structure of the keels and bare areas is similar to that of the keels on the lateral scales and the keels in *annectens* and *onca.* The scale surface adjacent to these regions is covered by spines with needle-like tips. The spines over most regions are 1.4–1.7 μ tall, but on scales 8 and 7 they are as tall as 3.2 μ and 2.4 μ, respectively.

COMPARISON WITH *ANOLIS AURATUS*

A. auratus has 22 subdigital scales (Fig. 15). Their distribution relative to the phalanges is quite similar to that in

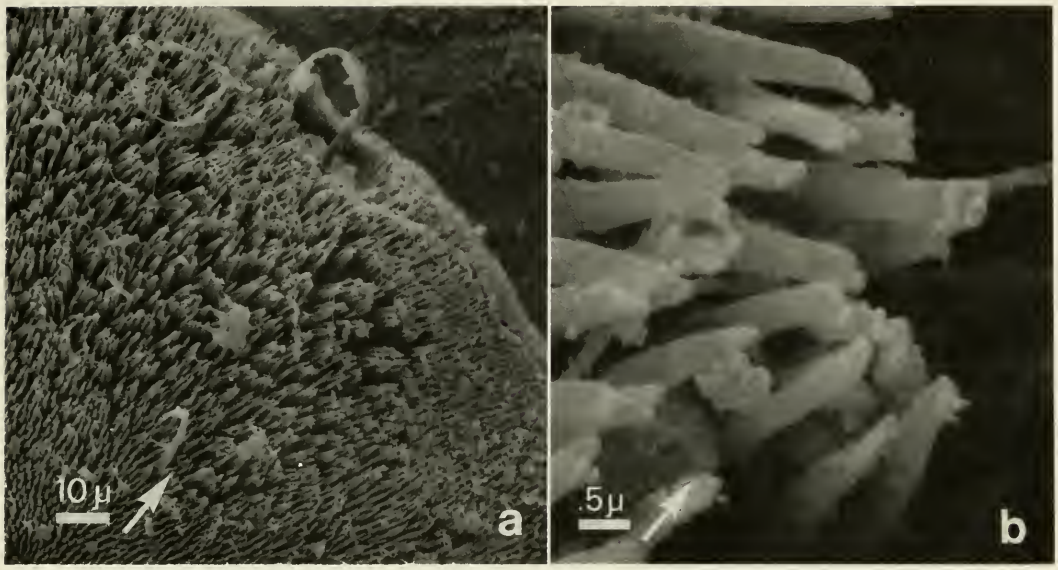


Figure 13. The morphology of scale 11 in *A. chrysolepis*. a) Shows the distal portion of the scale (Fig. 10) and the grade from spikes into the taller seta-prong intermediate morphology. b) Shows the flattened tip and frayed margin of the intermediate shape. Note that some of the tips appear to be bifurcated and not simply frayed.

A. annectens; the distribution in *auratus* versus *annectens* is: 1/1 claw base; 7/7 phalanx i; 8/6 phalanx ii; and 6/6 phalanx iii. Overall toe length, individual phalangeal lengths (phalanx ii is 1.3 mm in *auratus* and 1.4 mm in *annectens*), and scale sizes are very similar in spite of the smaller body size of *auratus* (Table 1).

The *auratus* scales include a) lamellae (scales 9–15), b) generalized subdigital scales (scales 7, 8, 16–22), and c) intermediate scales (scales 1–6).

a) The lamellae are grossly similar to those in *annectens* (apart from the absence of small lateral keels and bosses) and *chrysolepis*. The series of lamellae particularly resembles *annectens* in forming a narrower pad which is not clearly set off from the distal scale series (the "Norops" condition;[1] Figs. 1, 15, 18).

The lamellae are covered with setae (Fig. 16). The seta stalk is shorter than that in *annectens* (mean height over the front half of the lamella is 13.2 ± 0.5 μ; maximum height is 15.7 μ; height at the distal margin is 12 μ), but the orientation, stalk diameter (0.55 ± 0.06 μ), and spatular dimensions (base [width] 0.60 ± 0.04 μ; height [length] 0.57 ± 0.04 μ; area 0.173 ± 0.020 sq μ) are similar to those in *annectens*. The spatula is slightly less broad than that in most West Indian *Anolis*.

[1] The "Norops type condition" was defined by Williams (1974: 17) as "loss of distinctness of the anterior margin of the pad (that under phalanx ii) as against the scales under phalanx i" and was regarded as the third morphological stage in a sequence of "retrograde evolution." The present study has shown that the condition depends upon the absence of one or more small scales deep to the pad at the ii/i interphalangeal joint. These scales, when present, "raise" the first phalanx relative to the pad (*Anolis* condition *fide* Boulenger, 1885: 11); in their absence the pad is "not raised" (Norops condition *fide* Boulenger, p. 95). The two conditions are less sharply distinct than Boulenger believed, although the end points of the series are indeed conspicuously different. Also, as we shall show below, the "Norops type condition" is not, as Williams (1974) supposed, truly retrograde in the sense of any loss of adaptive or even adhesive value; it is instead an *alternative* adaptation.

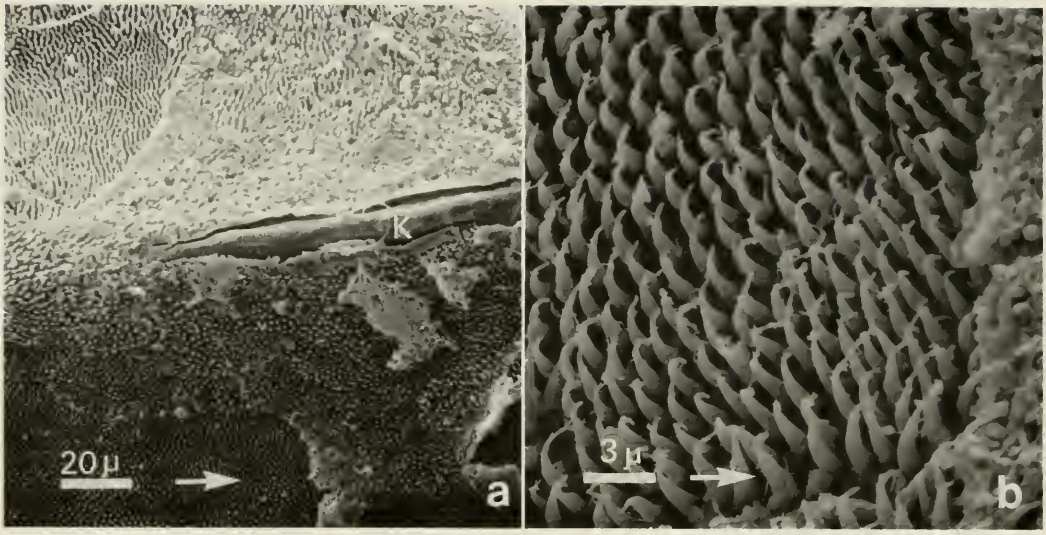


Figure 14. Scale 8 in *A. chrysolepis.* a) Shows a keel "k." b) Shows spines. This fine structure is typical of scales 1–8.

b) Scales 7, 8, and 17–22 resemble the generalized subdigital scales (non-lamellar and unkeeled) in *chrysolepis* and are unlike any of the scales in *annectens.* Scales 8 and 17 (Fig. 15) which flank the series of lamellae are more laterally expanded and could be considered lamellae except that the distal border is not thin and frayed.

All of the scales in this group bear setae (Fig. 16). The stalk height, particularly maximum height, is less than that of setae on the lamellar scales, but the other dimensions are not different. The setae are distributed over the central and distal regions of the scale. Proximally and laterally the morphology grades into prongs, spikes, and finally spines. The fine structure of the scales is generally similar to that of the proximal scale series (scales 22–29) in *chrysolepis.*

c) *A. auratus,* like *A. annectens,* has individual scales with an unusually heterogeneous fine structure which combines the keels or bosses of multicarinate scales with the setae typical of lamellae. In *auratus* these intermediate scales extend from the claw almost to the pad.

Grossly, the intermediate scales (scales 1–6; Figs. 15, 18) have a fairly robust distal margin and well-developed keels. A few bosses occur over the median portion of the distal margin on scales 2, 3, and 4, but keels occur on all the scales. From one to four pairs of keels are present in median-lateral (on scale 3 only), lateral, far lateral, and extreme lateral positions (Fig. 18). The number of keels along the side of the toe is relatively constant, but their distribution on the subdigital versus the lateral digital scales differs. Excluding the median-lateral keel, the number of keels on the subdigital scales increases from proximal to distal as the subdigital scale expands around the phalanx. Proximally (e.g., scale 6) only the lateral keel

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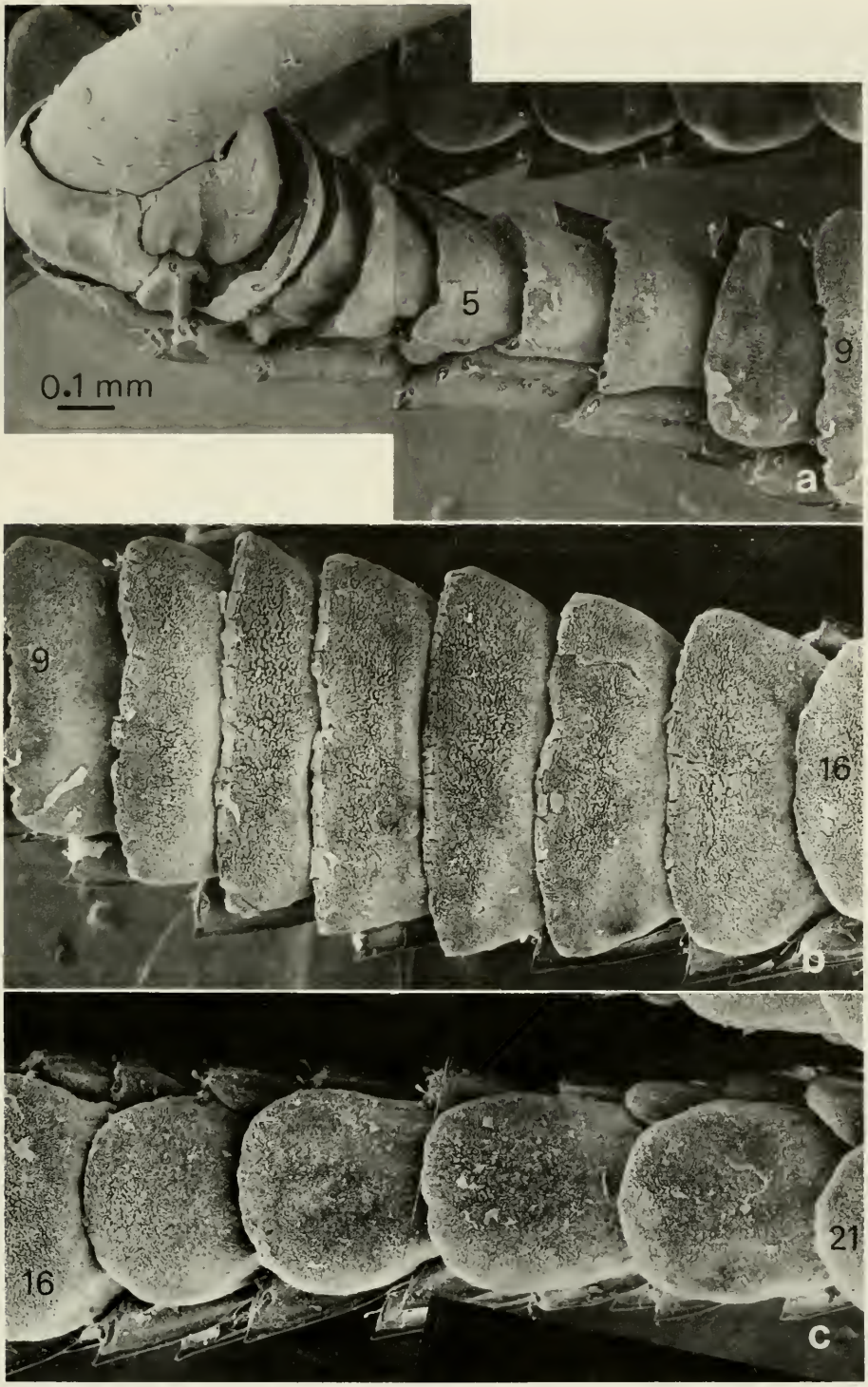
Figure 15. The third toe in *A. auratus.* The phalanx i(a) and ii(b) regions match at scale 9; the phalanx ii(b) and iii(c) regions match at scale 16. Note the difference in morphology of the distal borders of scales 15 and 16.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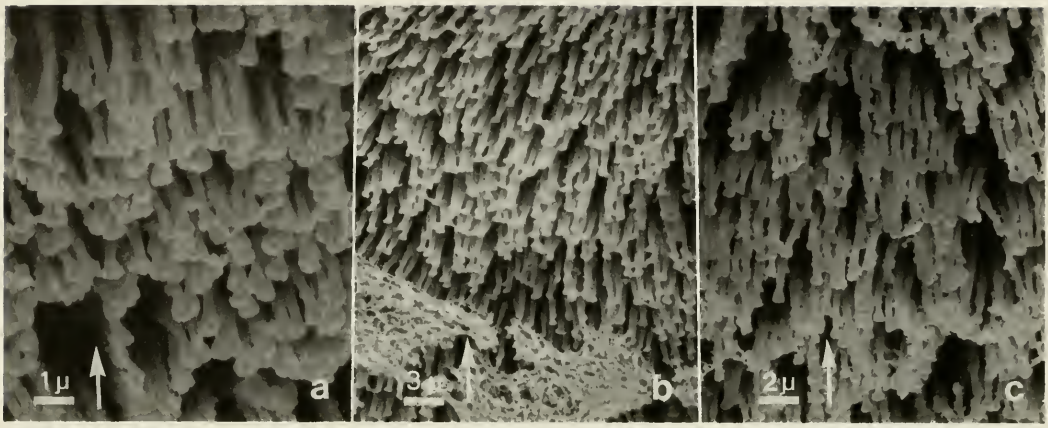

Figure 16. The setae in *A. auratus*. a) Illustrates setae on the fourth lamellae (scale 12). b) Illustrates setae on the claw base (scale 1). c) Shows setae on scale 21 just distal to the metatarsal-phalangeal joint.

is present on the subdigital scale, while the lateral digital scale is multicarinate. Distally (e.g., scale 3) where the subdigital scale wraps 180° around the phalanx, all three pairs of lateral keels (plus an additional median-lateral keel) are present on the subdigital scale, while the lateral digital scale is small and unicarinate.

The fine structure of the subdigital keels and bosses is comparable to that in *annectens*, adult *onca*, and *chrysolepis*. But there is a major difference in keel placement. In those species, a median keel is present and often the dominant scale feature. In *auratus* the homologous central region of the scale is covered with setae (Fig. 17). The dimensions, density, and orientation of these setae are comparable to those of the lamellar setae (with the possible exception of stalk height, which may be reduced). The setae grade into prongs and tall spikes adjacent to the lateral keel. Over the lateral region of the scale, including the zones between the keels (e.g., the lateral and far lateral keels), the scale surface is covered with spikes and prongs.

While the combination of features, particularly the grade from setae to spines to keel, is very similar to that on scale 9 in *annectens* (compare Figs. 5 and 17), there are some interesting differences. 1) In *annectens* the grade from setae to spines occurs on the medial side of numerous bosses scattered along the distal margin of the scale. The field of setae is much less coherent than in *auratus*. 2) The spikes and prongs are numerically dominant on the transitional scales in *annectens*, while in *auratus* the setae are much more common.

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Figure 17. The morphological grade from spikes to setae adjacent to the keel on scale 1 in *A. auratus*. a) Illustrates an oblique view of the scale, claw "cl" and keel "k" position. The "[ ]'s" indicate the position of the transect which begins at the left of (b) and continues to the right through (c). The (b) and (c) sections fit together at the point indicated by the "x." Spikes and prongs are mixed through (b). At the left in (c) are prongs grading into the seta/prong intermediate shape and finally setae at the far right. The grade continues to the right of (c), toward the center of the scale, as the spatulae become broader (see Fig. 14b). The difference between morphotypes can be most readily seen by comparing regions which are far apart (e.g., the right of [b] and [c]) and using Fig. 21 as a guide. The gradation of one morphotype into another is clear in regions such as (c) center. The tip shapes in these regions are not readily classified.

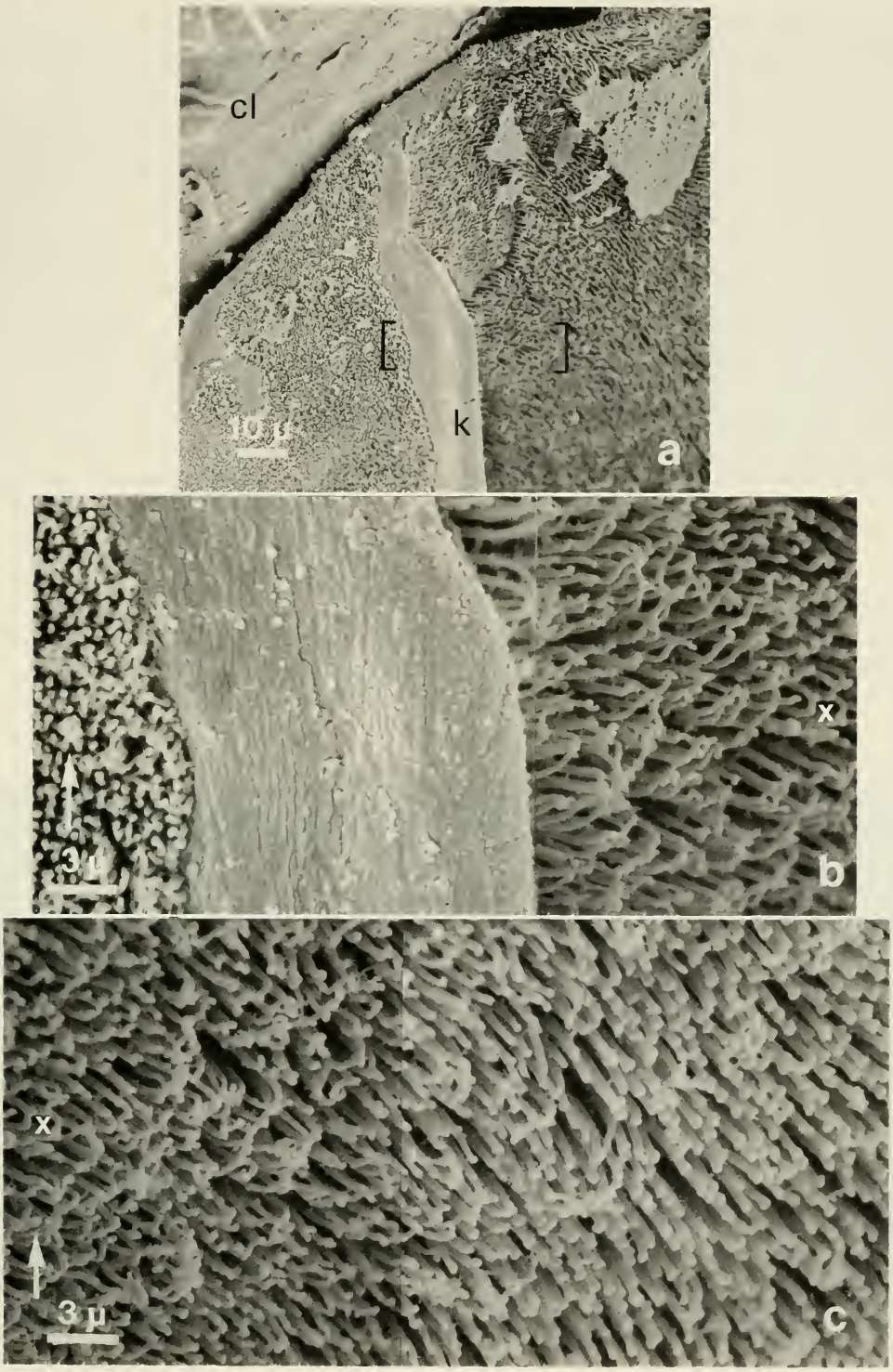

cl
k
10 μ
a
3 μ
x
b
x
3 μ
c

Figure 18. Distal portion of the third toe in *A. auratus*. Note the variation in keel number and placement in scales 1–7.

The lateral scales in *auratus* are multi- or unicarinate, studded with mechanoreceptors, and covered with spines. The spines occur in several sizes (Fig. 19).

DISCUSSION

Summary of the Comparative Data

The comparisons among *annectens*, adult and juvenile *onca*, *chrysolepis*, and *auratus* suggest that there are significant interspecific differences but relatively little novelty in subdigital morphology *per se*. The fine structure of setae, keels, spines, etc. is relatively similar among the species, and, in three of the species, the regional variation in structure approximates the range of interspecific variation. The dominant evolutionary pattern is change in the distribution of keels, setae, and spines relative to the phalanges.

If the species are arranged in the phylogenetic series proposed in the earlier paper (Williams, 1974), the major interspecific differences appear as trends for a) expanded setae distribution in *auratus* relative to *chrysolepis*, and b) the progressive substitution of multicarinate, spinate morphology for lamellae and setae in the *chrysolepis-annectens-onca* series (Fig. 20).

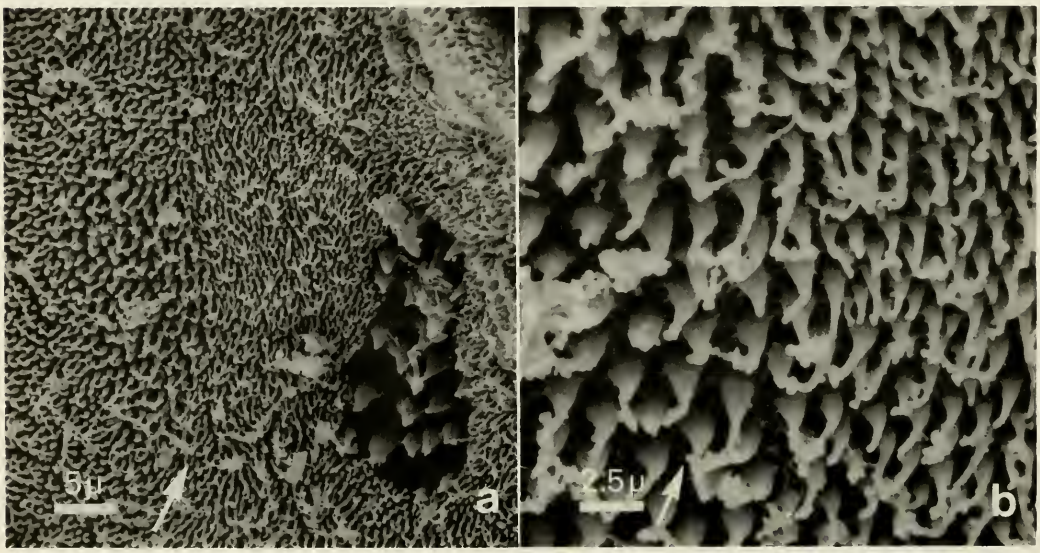


Figure 19. The diversity of spine shapes and sizes in *A. auratus*. The figures are taken on the infradigital scale adjacent to scale 5. a) Shows three spine sizes. b) Is a higher magnification view of the junction between two fields of spines.

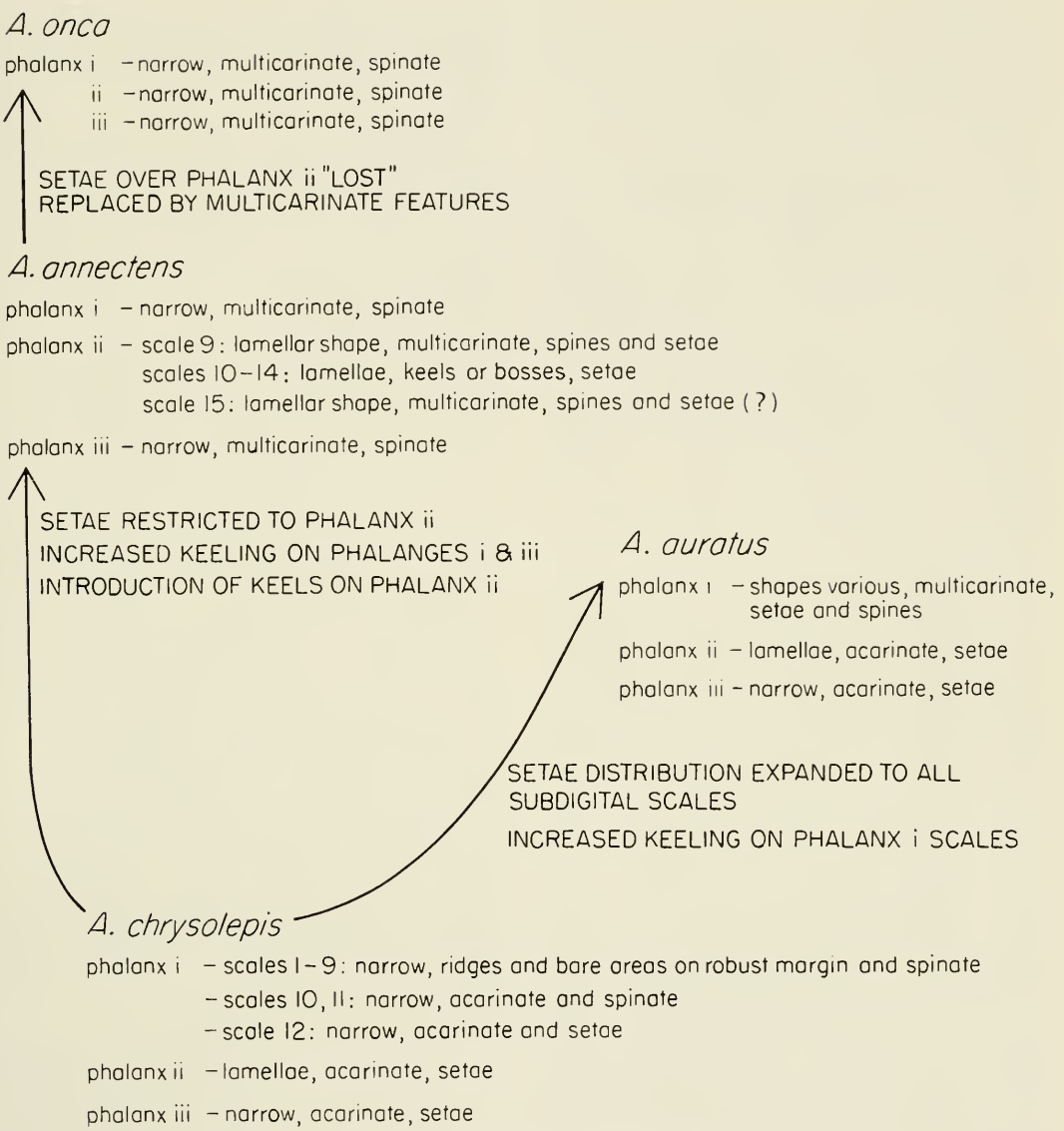


Figure 20. Summary of the comparative data.

Annectens differs from *chrysolepis* in three respects: a) the substitution of multicarinate, spinate scales on phalanx iii (scale shape is similar), b) the encroachment of multicarinate, spinate characters on the phalanx ii scales (the "lamellae" are slightly narrower, keels are present on the lateral portion of the lamellae, and the first and last "lamellae" are multicarinate with a surface dominated by spines and spikes), and c) the expansion of the multicarinate, spinate morphology to all the phalanx i scales.

Adult *onca* goes beyond *annectens* only in the morphology of the phalanx ii scales. The lamellar scales and setae have been replaced by narrower, multicarinate, spinate scales.

The presence of an almost pad-like scale series in juvenile *onca* along with the existence of a unique *annectens* specimen places particular importance on the similarities and differences among *annectens*, adult *onca*, and juvenile *onca*. The subdigital morphology of juvenile *onca* resembles the adult morphology in several respects: a) in the number and distribution of the scales, b) to some extent in the shape of the scales, c) in the correspondence between ridges in the juvenile and keels in the adult, d) in the absence of lamellae and setae, and e) in the poor differentiation among phalangeal regions. The morphology of the juvenile *onca* differs from that of the adult in a) the absence of definite keels, although scale contouring in some regions is pronounced, and b) the presence of tall spines, spikes, and prongs. In the first of these differences, the juvenile morphology is more conservative in terms of the proposed phylogenetic series than that of *annectens* or even *chrysolepis*, which have keeled subdigital scales. The absence of well-developed keels in juveniles may not be unique to *onca*. *A. cristatellus* adults have marked keels and bare areas in the phalanx i region while hatchling-sized (28.7 mm SVL) *cristatellus* have spine-covered ridges like those of *onca* juveniles and a few bare areas which are not associated with the ridges. Most of the contours on the lateral scales are also covered with spines as in juvenile *onca*. In the second of the differences relative to adult *onca*, the juvenile morphology is less conservative than that of *annectens* which has the complete spine to seta series and definite lamellae (see below and Fig. 21).

There is little resemblance between juvenile *onca* and *annectens*. In both forms the spine-seta series is more complete than in adult *onca*, and there is some regional differentiation in the subdigital scale series. But neither of these parallels translates into a convincing similarity between juvenile *onca* and *annectens*. For example, the differentiated region in juvenile *onca* is not synonymous with any of the regional series in *annectens*.

It is highly implausible that *annectens* is an "unmetamorphosed" *onca* hatchling. Juvenile *onca* are more similar to the adult *onca* than they are to *annectens*, *chrysolepis*, *auratus*, or generalized "Norops" species (e.g., *A. tropidonotus* and *A. notopholis*).

Clearly juvenile *onca* displays still another morphology intermediate between more generalized anoles, such as *chrysolepis*, and adult *onca*. Indeed, the implications of *annectens* and juvenile *onca* for a "retrograde" sequence are contradictory. *A. annectens* morphology implies a sequence in which robust keels invade and progressively replace setae and lamellae. In contrast, juvenile *onca* morphology would appear to imply that a substantial "retrograde" shift in the spine to setae series (see below) and dedifferentiation of the pad occur prior to the appearance of definite keels.

The juvenile *onca* morphology is an ontogenetic adaptation. It may or may not also represent a phylogenetically intermediate morphology in the "retrograde" sequence. We discuss these alternatives in light of additional functional and comparative considerations in the final paragraphs of the discussion.

The Morphological Series

The extraordinary diversity in subdigital scale morphology may be related to the wealth of structural intermediates and to the poor correlation among the characters. These factors result in a myriad of possible character combinations for a given scale. Setae occur not only on lamellae but also on narrow multicarinate scales. Keels occur on lamellae as well as on scales with a robust distal margin. Some "generalized subdigital scales" bear setae while others which are not otherwise different do not. This particular group of species may exhibit more

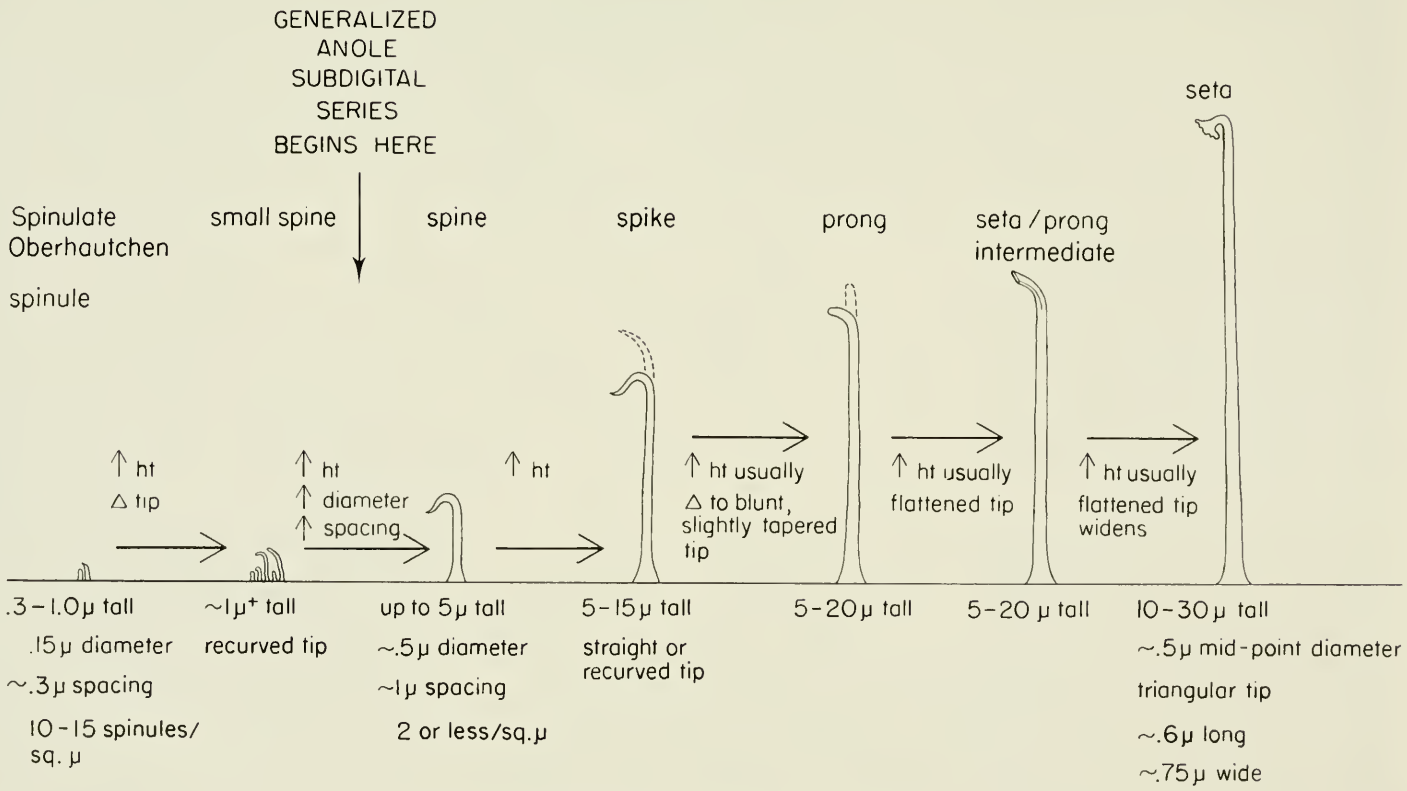
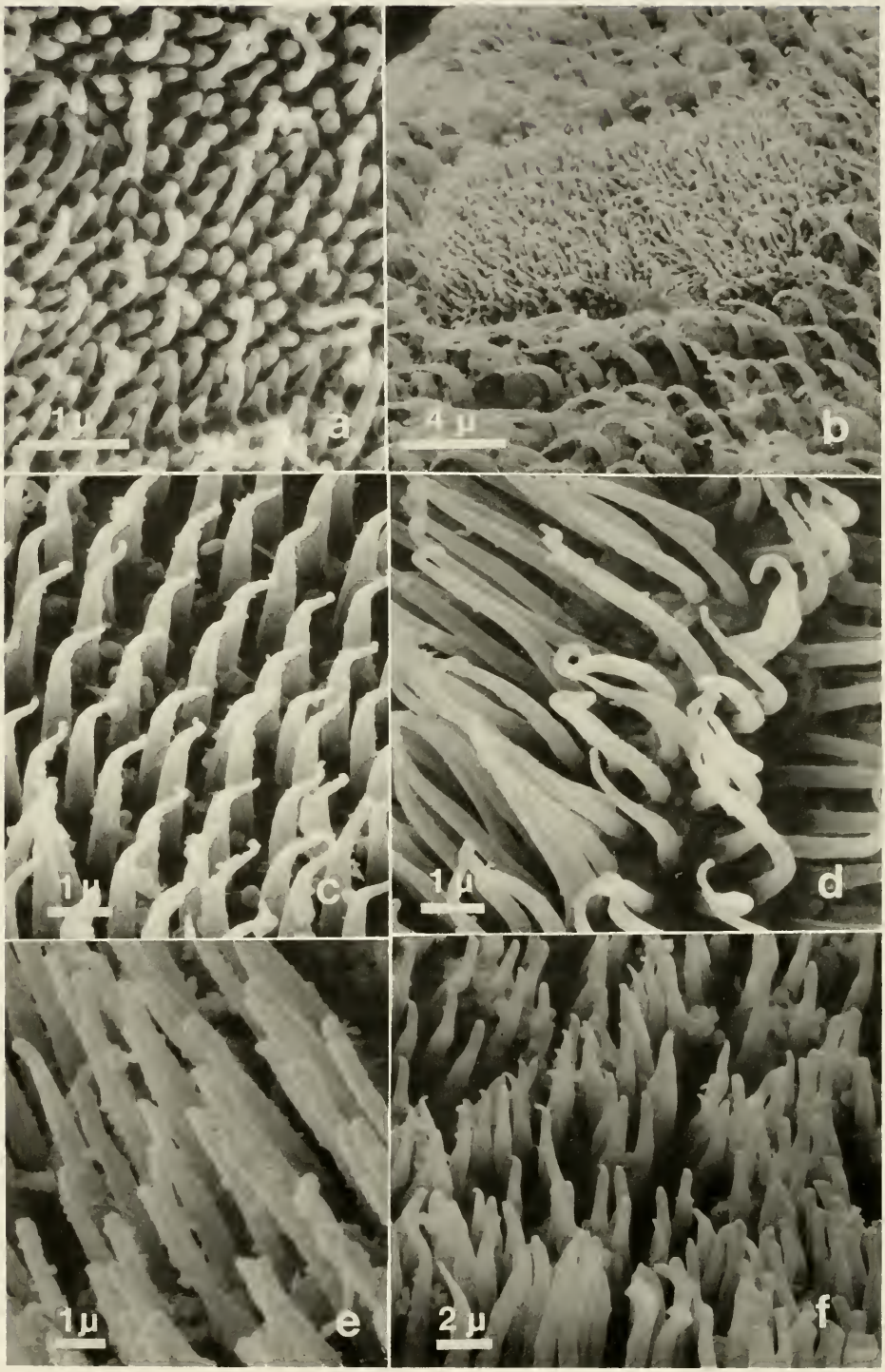


Figure 21. The morphological series of spine to seta.


1 µ
a
4 µ
b
1µ
c
1µ
d
1µ
e
2 µ
f

"creativity" in character combinations than most anoles, but their morphology is a cogent argument for the existence of more than one morphological series or character suite in the evolution of scale morphology.

The diversity in scale morphology appears to be interpretable in terms of three semi-independent morphological series, each one operating within a different dimensional range. These are: gross scale shape, contouring of the scale surface by keels, hillocks, etc., and fine structural specialization of the Oberhautchen (i.e., the spine to seta series; see Figs. 21, 22, 23).

Gross Scale Shape

Gross scale shape is determined by the length/width dimensions of the scale, the character of the borders, the cross-sectional shape, and the junctions with adjacent scales. In the present context our concern is the differentiation between lamellar and non-lamellar scales in anoles (A. Russell informs us that lamellar morphology in geckos is different). Lamellae are highly specialized scales, but they can be defined rather simply by the presence of a frayed, thin distal border and a length/width ratio <1. Both features are required to characterize lamellae. Wide scales with a robust margin occur fairly frequently, particularly adjacent to the claw and interphalangeal joints (e.g., *auratus* scale 3), but with rare exceptions (e.g., the most proximal lamella in *pulchellus*) all scales with a free, thin distal border are wider than they are long.

Scale Contouring

Variation in the surface contouring of scales can be arranged in a series based on increasing elevation and extent of the raised contours. The series begins with a relatively flat surface and extends to hillocks, which involve a single epidermal cell (e.g., Fig. 7), to ridges and bosses, and finally to keels. The hillock morphology apparently occurs only over the proximal and central portion of the scale. It is not clear that the hillocks are homologous with the rest of the series. Ridges, which extend into the central portion of the scale, and bosses, which occur adjacent to the distal margin, appear to be small keels. While both these features usually have a bare, smooth surface, the ridges, at least, may be covered with spines as in juvenile *onca*.

The Fine Structural Series: Spine to Seta

The *Anolis* Oberhautchen has spinules (Fig. 22; Ruibal and Ernst, 1965; Ruibal, 1968; Maderson, 1970). Such spinules are the beginning term in a morphological series which can be described as follows (Fig. 21): a) the spinulate Oberhautchen (Fig. 22a) consists of spinules and knobs which are 0.3–1.0 μ tall, 0.15 μ in diameter and about 0.3 μ apart (or 10–15 spinules/sq μ), b) the small spine (Fig. 22b center), which differs from the spinules by greater stalk height, a curved, more tapered tip, and reduced density (only some spinules are longer; see discussion following), c) the subdigital spine (Fig. 22b, c), which is marked by the absence of an understory of spinules, increased

←

Figure 22. a) The spinulate Oberhautchen from a dorsal digital scale in *A. evermanni*. b) Is taken on a lateral digital scale of *A. eugenegrahami* at one-quarter the magnification of (a). The central patch of small spines with a spinule understory has the same diameter and overall density as the spinulate Oberhautchen. The adjacent larger spines illustrate the diameter and spacing features which are typical of the subdigital spine/seta series. c) Illustrates fairly tall spines in *A. pulchellus*. d) Shows the even taller spikes in *A. evermanni*. Prongs are shown in the lower right of (e), and a few seta-prong intermediates are visible in the upper center of (e). The specimen is *Anolis* sp. n. near *eulaemus*. f) Shows a heterogeneous field of spikes, prongs, and seta-prong intermediates in *A. cuvieri*.

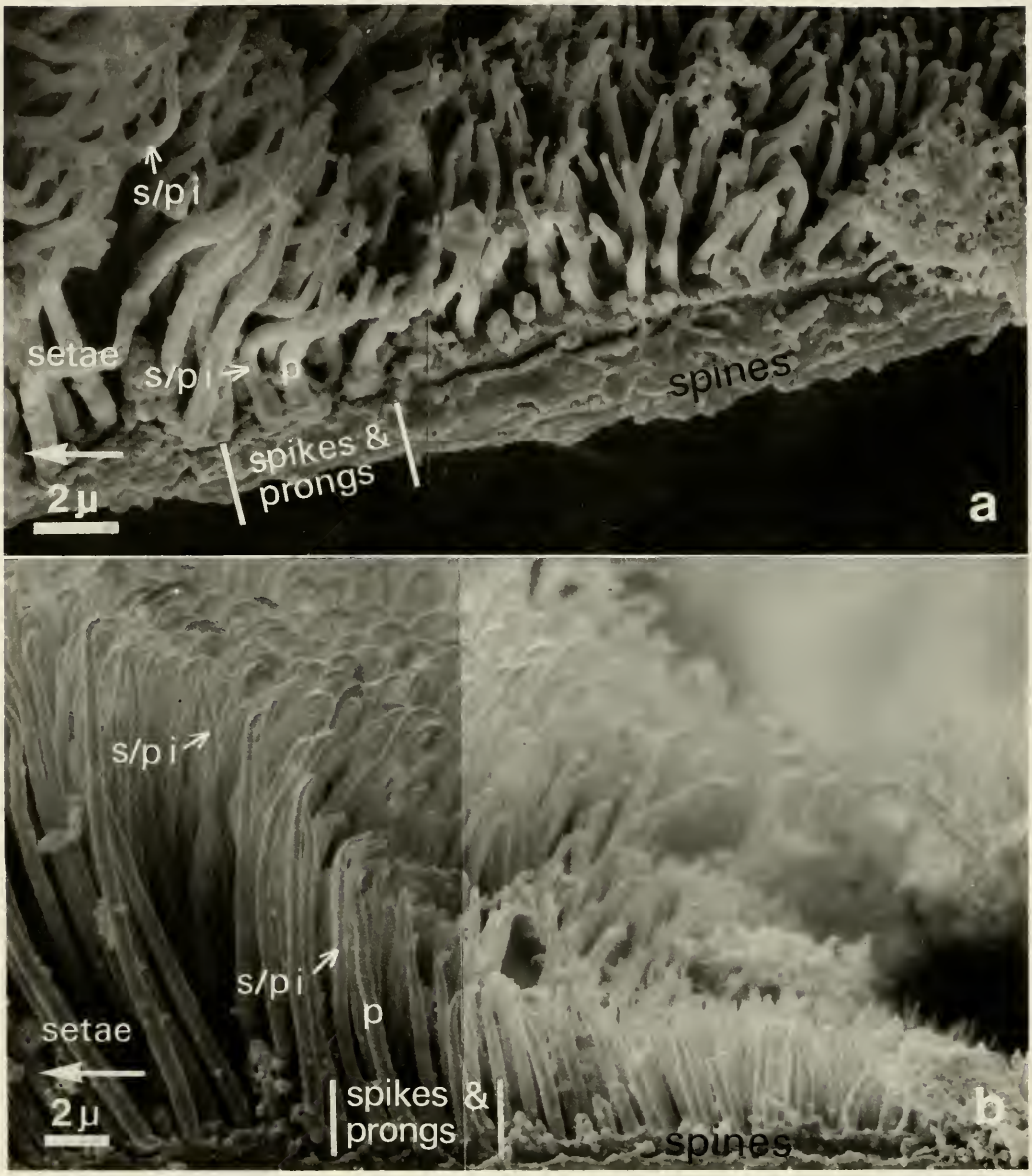


Figure 23. The subdigital spine to seta morphological series in *A. evermanni.* The figures are taken in the proximal portion of lamellae 8. The toe has been sectioned proximodistally. a) Is a ventral view at a slightly larger magnification than the lateral view (b). In this particular specimen the hook tips are not strongly recurved or highly tapered (cf. Fig. 20) so that the spike morphology is not well shown. The seta-prong intermediate "s/pi" shape is shown along the section margin and lateral to the margin (see also Figs. 13 and 20). A prong, "p," is also indicated. Setae significantly increase in height distal to the figure margin.

diameter of the stalk (about 0.5 μ at the midpoint or base, if the stalk is very short), decreased density (2 or less/sq μ; spacing about 1 μ), and often increased height (up to 5 μ), d) the spike (Fig. 22d), which differs from the spine by increased stalk height, e) the prong (Fig. 22e, f), which has a blunt or curved, but almost untapered tip, f) the seta-prong intermediate (Figs. 22e, f, 13b), in which the prong tip is dorso-ventrally compressed and stalk height is often greater, and g) the seta (e.g., Figs. 4, 11, 16, etc.), in which the flattened tip is expanded into a spatulate, triangular shape (the spatula is about 0.75 μ wide by 0.6 μ long). Several of the morphologies in this series may occur within the borders of one epidermal cell, and generalized anoles usually have all members of the series. Subdigital scales usually exhibit only the terminal (right) portion of the series (c–g). The structural series between spines (c) and setae (g) typically occurs in the proximal portional of lamellae (Ruibal and Ernst, 1965; Fig. 23). The spinule/spine portion of the series (a-c) occurs on the lateral digital and body scales, although spines with the dimensions of subdigital spines are rare except on the lateral digital and plantar/palmar scales.

The spinule (a) to spine (c) series appears to model the transition from the spinulate Oberhautchen to the subdigital series. It involves alteration in the height and diameter of the spinules and a major change in their spacing or density. The spine (c) to seta (g) series is based on variation in stalk height and tip shape. Stalk diameter and spacing or density are relatively constant between the spine or spike and the setae. Russell (1976) proposed a morphological series for the origin of gecko setae based on interspecific variation in *Cyrtodactylus* which appears to show spine-spike-seta components. Dimensions apart from height are not indicated, so it is difficult to compare the two series in detail.

The aspinulate, bare areas are typical of major scale contours, but also occur in regions with no relief (Figs. 8, 9). The relationship of this Oberhautchen specialization to the spinulate series is unclear. In fact, the surface morphology of these bare areas is unlike any of the three generalized Oberhautchen types (spinulate, lamellate, or dentate) described by Ruibal (1968) and Maderson (1970). A number of observations suggest that the morphology is not an artefact of the shedding cycle nor produced from a spinulate Oberhautchen by wear. a) The bare areas are often slightly raised or elevated relative to the plane of the adjacent spinate areas—they are not worn down. b) The immediately adjacent spines do not show excessive wear. c) The bare surface is actually striated as if by use, and these striations do not occur in specimens where the Oberhautchen has separated postmortem. d) Limited comparisons (for West Indian species) suggest that there is consistency in the placement of these areas between individuals. The bare, smooth Oberhautchen morphology characterizes all of the subdigital scales in the primitive iguanid, *Morunasaurus groi* (Peterson and Williams, unpublished data). It is not clear whether this surface morphology is a specialization of and within the spinulate Oberhautchen series or whether it represents an even simpler and distinct Oberhautchen type. The problem is compounded by the difference and implied increase in bare areas between juvenile and adult specimens of *cristatellus* and *onca* (see Maderson and Williams, 1978, and in preparation, for discussion of *onca*).

Functional and Ecological Implications

Without actual behavioral and experimental data, discussion of the functional significance of variation within and among the three morphological series has to be limited. But we can construct and

evaluate a number of hypotheses on the basis of comparative data.

Possible Functional Significance of Lamellae

The Relationship between Lamellae and Setae

The shape of a lamella appears to reflect its function in bearing adhesive hairs or setae. Given that the density of setae is constant over the exposed portion of the scale surface, the number of setae is determined by the total surface area (more extensive data regarding this are given in Peterson and Williams, in preparation). Lateral expansion of the scales which bear setae produces the characteristic lamellar shape and, at least in the West Indian ecomorphs we have examined, is a major vehicle for adjusting the number of adhesive hairs to the body weight (loading) (Peterson and Williams, in preparation). There are, however, two additional and alternative means to vary seta number: a) change in the length of the phalanges which have setae-bearing scales (varying the length of the "pad" independently of lamellar number or pad width), and b) restricting or expanding the distribution of setae relative to the phalanges. It is important to note that packing more or less lamellae into a pad of a given length and width does not significantly alter the number of setae.

The relatively narrow pad of many anoles—*chrysolepis*, *auratus*, and *annectens* among them—would itself provide for fewer setae in proportion to the animal's body weight than in the West Indian ecomorphs unless the alternative adjustments are made. In *auratus*, where the pad is particularly narrow, the phalanges are long in relation to snout-vent length, and setae occur on all the subdigital scales (i.e., two compensating adjustments are made). Crude estimates of seta number (based on seta density and seta-bearing area) indicate that these adjustments more than compensate for the reduction in lamellar width. *A. auratus* has at least as many setae as an *A. evermanni* (a Puerto Rican trunk-crown ecomorph with a wide pad and many lamellae) of the same body size. The situation is rather different for *annectens*. While it is very possible that the ratio of setae/body weight might be altered without comprising essential function, the "safety factor" reflected in generalized anole ratios would have to be very great for the reduction in the *annectens* ratio not to have behavioral consequence. The restriction in pad width coupled with the short second phalanx (1.4 mm compared to 2.1 mm in a comparably sized specimen of *chrysolepis*) and the restriction in seta distribution to the second phalanx could mean that the setae would have to "cooperate" with other devices to support the animal.

Apart from the relationship with body size, the functional advantage of narrow lamellae is unclear. As suggested in the earlier paper, narrow lamellae may constitute a stage in pad reduction *per se*, but clearly they do not always imply a reduction in the number of setae (cf. again *auratus*) nor presumably decreased competence in adhesion.

Lamellar scale morphology probably also reflects adaptation for applying setae. Lamellar scales, particularly the thin distal margins, are unusually flexible and compliant. Flexibility of the scale along with the length of the seta stalk permit the spatulae to "find" the environmental surface and conform to a curved or otherwise grossly irregular substrate (Hecht, 1952, discusses lamellar shape in terms of pad flexibility; see also Hiller, 1968, and the discussion of seta function following). For a pad of a given size, an increase in lamellar number might permit the seta-bearing area to better conform to surfaces with a smaller radius of curvature. This aspect of lamellar function may partially explain the interspecific increase in lamellar number with increas-

ing perch elevation (and decreasing perch diameter) (Collette, 1955; Williams, 1974).

The lamellae of geckos (Dellit, 1934; Russell, 1975, 1976, 1979) receive the insertion of numerous tendons originating from the metatarsal-phalangeal joint capsules and plantar tendon system. Ultimately the tendons operate in series with the digital and ankle flexors. The specialized tendon arrangement coupled with the flexibility of lamellae have suggested to Hiller (1968) and Russell (1975, 1976) that lamellae have a dynamic role in applying setae. Russell (1975) argues that the subdivision of the pad into scansorial plates (i.e., lamellae) increases the effectiveness of the setae because each lamella can be individually controlled by the tendons. Once the setae tips "find" the surface, flexion of the lamellae via the tendons places the setae under tension and transmits force between the adherent epidermis and the skeleton (Russell, 1975). Hiller's (1968) hypothesis for seta function in geckos involves an initial application of the spatulae via an active flexion of the toes and lamellae. (Russell [1975] and Hiller [1968] also implicate inflation of digital venous sinuses, which are present in some geckos, in the adhesion process.)

Anole lamellae have a similar set of tendons (Peterson and Williams, unpublished data; Russell, personal communication). Given the morphology of the setae in anoles, tension exerted on the lamellae, which is produced as the foot approaches contact with the substrate and the digital flexor musculature fires to meet weight-bearing conditions, would wipe the distal edges or flattened expanse of the setae into the surface and establish the "grip" (see discussion of seta function). Once the "grip" is established, tensile stress can be transmitted from the setae/epidermis to the skeleton via the lamellar tendons as in geckos. If these hypotheses are correct, the internal morphology and flexibility of lamellae are significant adaptations for applying setae and transmitting tensile forces.

The function of lamellar tendons in transmitting tensile forces may also contribute to the correlation between lamellar number and body size (Hecht, 1952; Collette, 1955; Williams, 1974). Scaling for increased tensile loads could occur by an increase in tendon diameter or by an increase in the number of tendons (by increasing the number of lamellae). Tendon robustness does vary, but, at least in the West Indian anoles, the dominant pattern is to multiply the number of tendons (and therefore the number of lamellae). This pattern maintains a relatively size-independent lamellar area/tendon relationship while scaling total tendon cross-sectional area to total seta stalk cross-sectional area. A size-correlated increase in tendon diameter by itself would scale the cross-sectional areas of the load-bearing tissues, but drastically increase the lamellar area served by each tendon. Perhaps the role of lamellae and lamellar tendons in applying setae has required criteria of scaling similarity which include lamellar area.

An interesting caveat to the argument that setae and lamellae are functionally associated is the existence of setae on non-lamellar scales (or the converse—lamellae which do not bear setae). This occurs not only in *chrysolepis* and *auratus*, but in several West Indian and Central/South American species (Peterson and Williams, in preparation). The non-lamellar setae are slightly different from typical lamellar setae. In *auratus* the stalk is shorter. In *chrysolepis* the stalk is shorter and less tapered, and the spatula is somewhat narrower. But, in each case the range of variation in lamellar setae includes these morphologies. Unless very similar seta morphology can function in a totally different fashion on lamellar and non-lamellar scales, the flexibility, compliant margin, and internal tendons of lamellae

are simply not necessary for seta function.

There are several possible, complementary explanations for the variation in distribution of setae compared to lamellae. a) Pad morphology (i.e., lamellae) might be less effective in positions adjacent to the claw or sole of the foot. In some anoles the pads extend to the sole, but lamellar morphology does not seem to occur in the phalanx i region of any anole (cf. geckos; Russell, 1976, 1979). b) If there is a necessary relationship between external lamellar morphology and internal digital tendons, the distribution of lamellae might be limited to certain phalanges by constraints on the distribution of the tendons. There are a number of potential mechanical constraints on extending tendons into the phalanx i region. For example, long tendons which are not controlled by a retinaculum or placed very deeply in the toe could act not only on their lamella of insertion, but "bowstring" or alter the more proximal pad contour and disengage setae. The arrangement in geckos (Russell, 1975, 1976) appears to avoid this problem with a deeper placement of the tendons and a more conservative (distal) branching of the tendons serving individual lamellae. But it is also interesting that the terminal and basal pads in several gecko genera are associated with separate internal tendon systems (Russell, 1976). Any of these "potential constraints" beg the question of an altered tendon origin and arrangement in anoles, but nonetheless, mechanical constraints may be operating to limit the distribution of lamellae to certain phalanges. c) Lamellar morphology may increase the effectiveness of setae by engaging more of them, but the advantage of lamellar setae may be significant only on certain environmental surfaces. Both the number of lamellae (Collette, 1955; Williams, 1974) and seta distribution relative to the lamellae (Peterson and Williams, in preparation) appear to be related to the environmental surfaces used by the species. There is an enormous diversity in the architecture of vegetational surfaces ranging from the waxy rubble, often trichome-studded surface of deciduous leaves to the grooved and "rough" surface of grass blades, to the very gross surface relief of cork and older bark (Martin and Juniper, 1970). While the claws probably contribute most of the grip on rough bark, setae appear to be responsible for purchase on very dissimilar cuticular surfaces, e.g., on grass blades and herbaceous leaves. The grass anole, *A. auratus*, has at least as many setae for its size, fewer lamellae, and a high proportion of non-lamellar setae compared to ecomorphs which use leaf, stem, and twig vegetational surfaces. The functional association between lamellae and setae presumably is reduced in *auratus*, suggesting that lamellae may not be as advantageous on grass as on most herbaceous leaves. Considerably more data on plant cuticles, setae, and setae/lamellae distribution are required to approach this problem, but the functional advantage and significance of lamellar morphology may vary with the properties and fine structure of vegetational surfaces.

Implications for the "Retrograde" Series

This general discussion suggests a framework for evaluating the morphological trends in the *auratus* and *annectens-onca* lineages. In both lineages the number of lamellae and pad area are reduced relative to *chrysolepis*, and the "Norops" condition appears. These morphological parallels are probably not indicative of precise parallels in behavioral and ecological specialization.

The functional significance of the "Norops" condition is unclear at this point. The distribution of the character within *Anolis* and its association with trends in fine structure are not readily interpretable. In the *annectens-onca* line the "Norops" condition is associated

with the invasion of multicarinate morphology into the phalanx ii or pad region, while in *auratus* it is associated with the expansion of pad or adhesive function into the phalanx i region. In both cases morphological differentiation of the phalanx i and ii regions is decreasing, but the effect appears to be functional divergence. The "Norops" condition, we emphasize again, is not invariably a "retrograde" change and an indication of decline in adhesive function.

While the number of lamellae and pad area in *auratus* are reduced relative to *chrysolepis*, they are comparable to those of West Indian grass anoles (e.g., *pulchellus*, where, however, the fine structure of the pad is different). Even if there were no data on the behavior and habitat preferences of *auratus* (Kiester *et al.*, 1975), there would be little basis to question the functional competence of the pad. The trends in *auratus* appear to represent body size and habitat specialization of the "adhesive" structures rather than selection for an alternative "non-adhesive" function.

The situation is different in *annectens*. If, as we have argued above, pad area is crudely indicative of the number of setae available to support the animal (in this species there are few non-lamellar setae) and lamellae variously function in applying setae, and if interspecific comparisons can be used to infer what the absolute values mean in terms of limits on adhesive behavior and vegetational habitat, then there are rather serious questions whether the *annectens* pad is functionally competent to support the animal. For its size *annectens* has fewer lamellae and less seta area than 1) grass anoles like *auratus* and *pulchellus*, 2) *chrysolepis*, which uses a wide range of vegetational surfaces close to and including the forest floor, and 3) the West Indian trunk-ground ecomorphs, such as *cristatellus* and *cybotes*, which often sleep on leaves, but climb and forage from the lower trunk (see also Kiester *et al.*, 1975). Among these more terrestrial, but still generalized anoles, there are no parallels for *annectens*. The morphology suggests that selection for "adhesion" based on setae is diminished in *annectens* and that the range of vegetation and behavioral repertoire of the animal are altered relative to generalized anoles. *Annectens* probably is much more dependent on its claws, and surfaces which will not accept the claw, like grass blades and leaves, may not be as readily used.

Possible Functional Significance of Scale Contouring

Contours as "Traction" Devices

Scale contours which are relatively rigid and permanent are probably "traction" devices which work with moderately large (on the order of 0.5 mm–1 mm) surface irregularities (e.g., on bark) or create such irregularities in loose sand or dirt. Keels, bosses, ridges, and even the distal margins of carinate scales will interdigitate with the gross surface irregularities of bark or terrestrial substrates, and the relative rigidity of multicarinate scales permits these contacts to transmit propulsive and reaction forces. Given irregularities of the proper size or loose sand or dirt, carinate scales will increase the static frictional coefficient of the contact between the foot and environment (Gans, 1974) so that more force can be transmitted across the contact without slippage.

The keel can transmit forces applied a) parallel to the toe if the distal end of the keel is engaged by an environmental contour, and/or b) perpendicular to the long axis of the toe if the crest of the keel is braced against an environmental contour. Both probably occur, and the ostensibly parallel keels on adjacent digits are able to "find" and exploit environmental irregularities with a variety of spatial orientations because the hind limb digits (1–4) are placed at angles of 30°–110° to the direction of motion (see also Robinson, 1975). The long third and fourth toes are

nearly perpendicular to the direction of motion (there is considerably greater diversity in arboreal postural positions). The interdigitating contacts created by the keels on these toes can very effectively transmit propulsive forces applied perpendicular and parallel to the direction of motion. The proximo-distal orientation of the keels may also be advantageous in providing traction as these toes rotate about their long axis during the propulsive phase (Laerm, 1973 describes this rotation for *Basiliscus*, but it occurs to some degree in many lizards). Keels are rotated into contact with the substrate during limb retraction, and like caterpillar or tank tread, could "find" or create contacts which maintain a high coefficient of static friction. In many terrestrial cursors (e.g., *Dipsosaurus*) and some forms that combine scansorial and terrestrial habits (e.g., *Enyalioides*) keel shape, placement, and relief often display a preaxial/postaxial asymmetry that is probably related to the long-axis rotation of the digits during the propulsive phase.

The Evolution of Multicarinate Scales in *Anolis*

An evolutionary trend to substitute contoured, multicarinate scales for uncontoured scales may represent adaptation for using environmental surfaces which would have low coefficients of static friction to a smooth scale. Low coefficients of static friction might arise for a smooth scale if the environmental surface is formed a) by particles with low cohesion (e.g., sand) or b) by rigid irregularities which offer too little contact area for the scale. The latter situation might occur on tree bark or branches. Whether it does or not depends on the relationship between the spacing of the surface irregularities and the dimensions of the digits. Keels and other contour features would appear to be advantageous for locomotion on bark surfaces where the distance between irregularities is somewhat less than the width of the digit or on sand. Keels may also represent adaptation for behaviors which rely on the rapid application of large forces, e.g., running. From these hypotheses one would predict that keels and related scale contours would characterize climbing, trunk-dwelling, and terrestrial species, but not those specializing in twig or smooth leaf surfaces. Among the West Indian anole ecomorphs, subdigital keels occur on some scales in the phalanx i region in the trunk-ground ecomorphs (i.e., *A. cristatellus*, *A. lineatopus*, and *A. cybotes*); in these species the other phalanx i scales have striated, bare areas along the robust curved margins of the scales. The keels and bare areas have somewhat more relief, but are generally similar to those in *chrysolepis* (Fig. 10). Both morphologies are absent in twig anoles, e.g., *A. valencienni* and *A. occultus*. The anole ecomorphs which use the trunk and large diameter branches, e.g., *A. distichus* and *A. stratulus*, lack subdigital keels, but have prominent bare areas on the phalanx i scales similar to those in *chrysolepis* and *cristatellus*. These contoured margins may be able to function like keels in increasing traction relative to forces applied parallel to the toe (e.g., digital flexion in a leap), but scale contouring appears to be less prominent in the more strictly trunk-dwelling species than in the trunk-ground ecomorphs. Keels are not present in the West Indian grass anole species we have examined (*A. pulchellus*, *A. poncensis*, *A. olssoni*, and *A. semilineatus*) although "bare areas" occur on some of the phalanx i scales.

Subdigital keels or marked scale contouring into ridges appear in several Central and South American anole species (e.g., *A. notopholis*, *A. tropidonotus*, *A. nebuloides*, *A. nebulosus*, *A. quercorum*, *A. liogaster*, and *A. dollfusianus*) which combine terrestrial substrates with perches close to the ground. The keels are confined to the phalanx i region and are comparable to those in *cristatellus* in

relief (the position of the keels on the scale and the distribution of multicarinate scales within the phalanx i area are quite variable).

The available intergeneric comparisons largely corroborate the pattern in *Anolis*. Multicarinate subdigital scales occur in many (e.g., *Agama agama*, *A. stellio*, *Dipsosaurus*, *Phrynosoma*, *Crotaphytus*, *Morunasaurus*, *Sceloporus*, *Enyalioides*, *Tropidurus*, and *Iguana*), but not all (e.g., *Diplolaemus* and *Lacerta viridis*), the terrestrial and terrestrial/scansorial lizards. The subdigital scales are acarinate in *Chamaeleo* and *Phenacosaurus*, which are slow moving and characteristically use small diameter, smoother surfaces similar to those used by *A. valencienni*. However, *Polychrus* shares these behaviors and habitat preferences and has subdigital scales which are crowded with low bosses and keels (Peterson and Williams, unpublished).

Although there are exceptions and the character of bark and terrestrial substrates is more complex than we can consider, the distribution of multicarinate scales is generally consistent with their role as a "traction" device and with adaptation for locomotion on surfaces which have a low coefficient of friction because of gross surface irregularity or the low cohesion of surface particles. Within *Anolis*, keels occur in species which use terrestrial substrates, but not in the more strictly scansorial or grass-dwelling forms (*A. auratus* appears to be an exception in possessing keels). The distribution of keels within the genus suggests that the trunk-ground structural habitat (broadly defined to include forms such as *chrysolepis*) might be the starting point for the elaboration of multicarinate features in the *annectens-onca* lineage.

It is interesting that trunk-ground anoles have limited keels and an adhesive pad while most other scansorial/terrestrial iguanids have multicarinate subdigital scales. The smaller body size of trunk-ground anoles permits them to use a broader range of vegetational surfaces than most of these iguanids. Leaves, twigs, and other grossly smooth vegetational surfaces are often used as sleeping sites or rarely as auxiliary perches. This greater repertoire of surfaces may make it advantageous to maintain the pad and introduce keels in only a limited area adjacent to the claw. The trunk-ground structural niche might begin to approximate the iguanid scansorial/terrestrial habitat with an increase in body size or in extreme xeric areas where a) the vegetation may be deciduous and the leaves are often too narrow and small to support the animals, and b) the presence of loose, sandy soil might increase selection for scale contours as "traction" devices. Body size is generally conservative among trunk-ground forms, but the West Indian ecomorphs offer two cases to examine whether scale contour features are exaggerated and the pad characters reduced when trunk-ground forms radiate into arid regions. These are: the radiation of Puerto Rican *cristatellus* stock into scrub forest as *A. cooki* and the radiation of Hispaniolan *cybotes* stock into thorn scrub forest as *A. whitemani* (Williams, 1963).

Comparison of *A. cristatellus* and *A. cooki* indicates no marked difference in the contour features of the phalanx i region and no contour features present in the phalanx ii and iii regions, although lamellar number and pad width appear to be reduced in *cooki*. Comparison of *A. cybotes* and *A. whitemani* reveals that some *A. whitemani* individuals have three or more robust keels on all the phalanx i scales while *cybotes* has laterally compressed scales with robust distal margins distally and two or three keeled scales proximally. *A. whitemani* shows no expansion of keels into the phalanx ii or iii regions, and there is no indication of reduction in lamellar number or pad size.

The multicarinate scales in *A. whitemani* combine the features of *annectens* and *onca*. Scale shape resembles the *onca* phalanx i scales rather than the long

cylindrical scales of *annectens* (Fig. 1b). The relief of the keels is less than that in *onca* and comparable to that of most *annectens* keels, but the lateral digital scales have many sharp, protruding keels as in *onca*. Hillock contouring between the keels and toward the base of the scale is comparable to that in *annectens*. The positions and relative development of the keels show no consistent resemblance to *annectens* or *onca*. The more proximal phalanx i scales have a dominant median keel and a pair of lateral keels. This is similar to the *annectens* phalanx iii pattern or *onca* scales at the interphalangeal joints. Midway between the claw and the pad the pair of lateral keels are dominant, and a second pair of lateral keels may be added. This is similar to *onca* scales in the mid-phalangeal regions. The most distal scales are similar in all three species.

A. whitemani occurs over a range of arid habitats. It can occur in the same general localities as *A. cybotes*. In these areas *cybotes* is found in small oases of trees adjacent to springs, while *A. whitemani* occurs in surrounding open dry scrub and out into sparsely vegetated areas (Williams, 1963). Extreme *whitemani* habitat is similar to that of *onca*. Unfortunately, our series of *whitemani* specimens is too small to examine the individual variation in subdigital keels in terms of habitat variation, but the appearance of robust keels in at least some specimens of a species which has radiated into sandy, extreme xeric habitat comparable to that of *onca* is striking.

The results of the two comparisons are inconsistent: each case is unique, and there are too few behavioral and ecological data to interpret their differences. But each appears to exhibit nascent trends which parallel the *annectens-onca* lineage: a) reduction in lamellar number and pad width in *cooki*, and b) an increase in the number and robustness of the keels in some specimens of *whitemani*.

It is, however, the coincidence of these trends which characterizes the *annectens-onca* lineage, and, to our knowledge, the *annectens-onca* lineage is unique among anoles in the combination of trends for pad reduction and marked expansion of multicarinate scales. If we view this combination of trends as an extreme in the spectrum of adaptation, rather than as a truly unique evolutionary pattern, the comparisons among anoles suggest the following interpretation of the evolutionary sequence in keel elaboration. a) A few low subdigital keels occur in the phalanx i region of a substantial number of anole species which use terrestrial substrates. These less "arboreal" or trunk-ground species also evidence narrower pads and/or reduction in lamellar number compared to trunk and canopy species of the same body size. Grass anoles may parallel the trend in pad reduction, but keels are infrequent. If, as is suggested by juvenile *onca* morphology, the "retrograde" sequence begins with pad dedifferentiation, then either grass or trunk-ground species might be the starting point for the radiation. But if, as is suggested by the *annectens* morphology, the "retrograde" sequence involves the progressive expansion of multicarinate features into seta-bearing areas, then the most probable starting point for the *annectens-onca* lineage is a trunk-ground habitat (broadly defined). b) To our present knowledge, multicarinate features are elaborated in only three anole species: *whitemani* (some individuals), *annectens*, and *onca*. In the cases where the general habitat associated with this shift is known, it is a xeric region. Although our survey has not been exhaustive, we have seen no evidence of keel elaboration in trunk-ground species with other habitat associations. *A. notopholis*, a mesic trunk-ground species, comes the closest to being an exception. In *notopholis* all but one of the phalanx i scales have long low keels. Keel position and relief is compa-

rable to that in *auratus*, and relief is much less than that in the *whitemani* specimens described above. Other ecomorphs, particularly grass (e.g., *auratus*, *poncensis*, and *olssoni*) and trunk (e.g., *brevirostris*) anoles, also radiate into xeric areas. With the exception of *auratus*, multicarinate scales do not seem to appear in xeric grass or trunk forms. Elaboration of multicarinate features in anoles is not always (e.g., *cooki*) or perhaps exclusively (e.g., *notopholis*) associated with the invasion of xeric regions by trunk-ground species, but there does appear to be some relationship among the habitat, ecomorph, and subdigital keels. c) Presumably the invasion of xeric areas translates into diminished selection for an "adhesive pad" (see the section on behavioral ecology of *onca*) and selection for scale contours which are more effective on lower friction surfaces like sand and rough bark. Continued or extreme selection for locomotion on these substrates might be correlated with the encroachment or substitution of multicarinate scales for seta-bearing lamellae in *annectens* and *onca*.

The Evidence from Non-Anole Iguanids and Geckos

Subdigital keels are relatively uncommon in anoles, but quite common in non-anole iguanids. Some insight into the habitat and behavioral correlates of keels can be gathered from the non-anole iguanids if we examine not the origin or appearance of keels, but the interspecific variation in keel shape and position. The comparisons among non-anole iguanids can be constructed to evaluate whether a) variation in keel shape and position is correlated with habitat differences similar to those implicated by the examination of anole species, and b) whether the multicarnate scales of *onca* and *annectens* are convergent on those of desert-dwelling iguanids. A complete survey is beyond the scope of this paper, but the comparisons which we have constructed as "test cases" proved quite interesting.

Enyalioides microlepis and *E. heterolepis* are mesic forest species which differ in the proportion to which they use bark and forest floor substrates (K. Miyata, personal communication). Keel shape and position are very similar in the two species.

The pattern of keel placement is also similar in two scansorial *Tropidurus* species: *T. torquatus*, from mesic open areas (Rand and Rand, 1966) and *T. occipitalis* from xeric coastal Peru (Dixon and Wright, 1975). Both species have a dominant median keel flanked by subsidiary lateral keels similar to the pattern in the *Enyalioides* species and on the phalanx iii scales of *annectens*. The xeric species, *occipitalis*, however, does differ from *torquatus* in several other features: a) the keel tips and crests are sharper, and b) keels on the lateral digital scales have more relief. These features and the morphology of the phalanx i region are convergent on *annectens*.

Scale shape and keel development are different in *Tropidurus peruvianus*, a xeric Peruvian coastal species which is predominantly terrestrial and lives on beaches, sand dunes, and boulders (Dixon and Wright, 1975). Keel asymmetry is marked in *peruvianus*, but there is a pair of dominant keels (probably the median and postaxial lateral) except at the interphalangeal joints where three robust keels (the median and the pair of lateral keels) are present. While the asymmetry and probable homologies of the keels are different, the emphasis on two robust keels rather than a single dominant median keel is similar in *onca* and *peruvianus*.

The more terrestrial, sand-dwelling iguanids which we have examined (*Crotaphytus wizlizeni, C. collaris, Dipsosaurus dorsalis, Phrynosoma* sp. and *Callisaurus*) resemble *T. peruvianus* and *onca* in having two, or usually more, relatively equal keels in lateral positions

rather than a dominant median keel (the homologies of the lateral and far lateral keels are not particularly clear because of torsion and asymmetry in the scales, e.g., *C. wizlizeni* has four or more keels all on the postaxial side of the scale).[1] In contrast, *Basiliscus vittatus*, a mesic cursorial/scansorial form, has a single keel that is asymmetrical in orientation. *Sceloporus olivaceus*, a xeric climber, has a robust median keel, although on some scales the pair of lateral keels are as large as the median. In *Iguana*, there are two relatively equal keels placed so close together in the median plane that they might well operate as a single keel.

The xeric terrestrial iguanids appear to have a larger number of keels and more robust keels in the lateral portion of the scale than the terrestrial forms in mesic habitats or than the more scansorial forms, which as a group emphasize a medially placed keel. This provides some corroboration of the relationship between elaboration of keeled scales and xeric habitats in *Anolis*. Presumably the aspect of xeric habitats which is functionally significant for subdigital scales is sandy or loose soil substrates. It is possible that the increased number and lateral placement of the keels are more effective in stabilizing sand to apply propulsive force while a single median keel is more effective on a curved surface or in working into bark crevices (a large number of keels acting on a rigid irregular surface would probably decrease the coefficient of friction by decreasing the area of contact or preventing keels from projecting into crevices). The xeric scansorial forms (*Sceloporus olivaceus* and *Tropidurus occipitalis*) utilize terrestrial substrates for foraging (Blair, 1960; Dixon and Wright, 1975), and both display an increase in keel number or robustness compared to mesic forms. This could be related to foraging on sand, but there may be other habitat differences, and the relationship is likely to be more complex.

The difference in keel placement between *annectens* and *onca* is mirrored in the difference between *Tropidurus occipitalis* and *T. peruvianus*, and the differences in subdigital scales between *occipitalis* and *torquatus* are generally convergences between *occipitalis* and *annectens*. The resemblance and comparative data are not complete enough to suggest a probable habitat and behavior for *annectens*. But the difference in keel placement and shape between *annectens* and *onca* appears to be significant in light of data from the non-anole iguanids. Quite apart from the difference in pad retention, the morphology of the mluticarinate scales suggests that *annectens* may be adapted for a somewhat different structural habitat than *onca*. Both pad retention and the morphology of the keels in *annectens* appear to indicate a more traditional anole structural habitat.

The most striking parallel for the substitution of a keeled surface for the adhesive pad may come from geckos. Russell (1976, 1979) describes the reduction or loss of subdigital pads in two groups of geckos which have radiated into xeric, sandy habitats. In these cases the pad is replaced by small, erect granular scales covered with spines similar to those in primitively padless, sand-dwelling forms (Russell, 1979). It is possible that the small, erect scales behave like individual keels and stabilize sand under the foot as propulsive forces are applied. Although

[1] Fringe-toed lizards such as *Uma scoparia*, *Acanthodactylus scutellatus*, and *Aporosaurus anchietae* are apparent exceptions to the generalization of greater keel numbers in sand-dwelling species. The subdigital scales in these forms are laterally compressed with a single median or median preaxial keel and subsidiary keels are absent. *Tropidurus thoracicus*, a relative of *T. peruvianus*, which even "sand swims" has similar subdigital morphology (Dixon and Wright, 1975). Presumably this morphology is adapted to trap sand between the "fringe" on the lateral digital scales and the subdigital keel.

Apparently there are a number of alternative adaptations which will increase the coefficient of sliding friction between the animal and a loose sand substrate (see also sidewinding [Gans, 1974]).

little is known of the behavior of these animals (they appear to be more terrestrial than *onca,* see Werner and Broza, 1969), the parallel reduction in adhesive structures in sand-dwelling geckos and anoles is striking. It is possible that sand injures or clogs the setae (Underwood, 1954, makes a comparable argument for forest floor geckos), but anoles in captivity do not appear to have any difficulty in climbing after walking or running over sand, and pad retention in the xeric trunk-ground species would suggest that sandy substrates do not strongly select against a pad and setae in anoles. We would interpret the trend in *Anolis* in terms of a) diminished selection for pad morphology in arboreal/climbing behaviors (also discussed in the subsequent section), and b) enhanced selection for keels and "traction" devices which are effective in loose sand or dirt.

Possible Functional Significance of the Spine to Seta Series

THE SPINE TO SETA SERIES: ADHESION OR PREHENSION

The morphological series in fine structure is remarkably continuous and almost certainly reflects the interface of developmental processes and function. In order to develop functional hypotheses for the differences reflected in the series, we will assume, for the present, that the morphological series is also a phylogenetic one and that the spinule morphology is a "starting point" for the subdigital series.

There appear to be two distinct portions of the series: the first involves the transition from the generalized Oberhautchen spinules to the subdigital spine-seta series (Figs. 21, 22), and the second comprises variation within the subdigital series (Figs. 21, 23).

The functional significance of the spinulate Oberhautchen is not well understood. The spinules may represent adaptation for protection from physical abrasion (Ruibal, 1968), the diffusion of some wave lengths of radiant energy (Porter, 1967), facilitation of shedding (Maderson, 1970), and/or some yet unappreciated factor.

The transition from the spinules to the subdigital spine-seta series might have occurred in response to selection for greater abrasion resistance, but this would not seem to explain the acquisition of a recurved tip. It is more likely that selection for purchase or grip is responsible. Initially, the spinulate surface itself might in some fashion interdigitate with the environmental surface and increase the frictional coefficient of the contact. The longer spinules (see Fig. 22a) might even be able to engage environmental irregularities like small hooks (the "velcro" principle). Selection to augment the microscopic prehension or interdigitation of some of the spinules could result in exaggeration of the stalk height and acquisition of a recurved, more hook-like tip (e.g., the small spine morphology shown in the central portion of Fig. 22b; note in the figure that not all the spinules have been exaggerated into small spines: there is an understory of very short spines and knobs similar to those shown in Fig. 22a). Presumably the height increase is selectively advantageous because a consistent increase in stalk height would produce too dense a "pile" for the tips to function. The selective increase in height establishes or aggravates a functional differentiation between spinules in the understory which do not function in prehension and small spines which do, and it alters the functional density. The spinules in Fig. 22a occur in a density greater than 10/sq μ; the small spines (excluding the understory in Fig. 22b) are about half as dense. Continued selection for prehensile, microscopic hooks could then result in increased stalk height to augment the effective range of the hook and in increased diameter to tolerate larger tensile loadings. The increase in stalk diameter is

necessarily linked with reduction in density and occurs at the expense of the spinules in the understory. The generalized subdigital spine morphology is reached with a height of at least 1 μ (usually greater, see Figs. 22, 23), a diameter close to 0.5 μ near the base, and a density of 2 or less/sq μ.

The collective alterations involved in the shift from spinules to subdigital spines could create a "prehensile" scale surface capable of augmenting the claw. It might augment the claw in such a way as to permit acrobatic and perch-walking maneuvers over a wider range of substrates. The effect of a "prehensile" scale surface would presumably be least on the tree trunk and greatest in the bush/canopy branch and twig zones where the surfaces accept the claw less well and the radius of curvature of the perch is small. Some of the foot positions which anoles use in acrobatic maneuvers on small perches would not be possible unless some grip independent of the claw were permitted. If spine-covered subdigital scales, like the series of phalanx i and iii scales in many anoles, could contribute to grip, the shift from spinules to the subdigital spine series would have significant impact on the range of vegetational surfaces and the repertoire of behaviors.

Hiller (1968) argues that, while the spine tip might behave like a microscopic hook, the behavioral significance of spines is negligible. His argument is largely based on experiments with geckos adhering to a series of artificial surfaces which are much smoother than twigs or branches, and probably too smooth for the small number of spines present to develop much gripping force (these experiments are discussed in more detail below). Sanding of the surface to roughen it resulted in a slight increase (value not reported) in the gripping force (Hiller, 1968). It is simply not clear that Hiller's (1968) objection would hold for natural surfaces or if major portions of the subdigital surface were studded with spines.

Within the anole subdigital series there are two trends operating to create the different morphologies: one in stalk height and one in tip shape.

1) The variation in stalk height is continuous and not closely correlated with tip shape (e.g., the sharp, recurved tip and spatula occur over a significant range of stalk heights). Stalk height affects the independence of the tip from the scale surface. A longer stalk permits the tip a greater range of positions and increases the odds that the tip will contact the environmental surface. Because the stalks are stressed in tension, variation in their length does not alter their strength nor require a compensatory change in diameter (Peterson *et al.*, in preparation). While there is no purely mechanical disadvantage or cost associated with increasing stalk length, presumably there is a developmental and material cost. Exceptionally long stalks would also be more likely to tangle and trap debris, and the properties of the keratin would have to be such as to maintain the tip orientation relative to the scale surface regardless of stalk length.

The longest stalks generally occur on lamellar setae (there is significant interspecific and regional variation in setae stalk height; Peterson and Williams, in preparation). The length of the stalk coupled with the flexibility of the lamellae permit the spatulate tips to reach surfaces which have a small radius of curvature or are irregular at the ultrastructural level (see discussion of tip function following). This is an extremely important aspect of seta function in anoles because the total number of spatulate tips is not particularly high (cf. the branched setae of geckos) and the total area of the spatulae is actually less than that of the underlying lamellae (Peterson and Williams, in preparation). The advantage of setae regardless of their mechanism is not exclusively in

the area or number of tips which they offer to the environment, but in the ability of those tips to "find," mold to, and engage the substrate, and this substantially depends on the dimensions and properties of the stalk.

Short stalks occur in narrow zones on the periphery of seta, prong, or spike-covered areas (Fig. 23), often where the scale surface is shadowed by another scale, and occur widely over the surface of more rigid, often contoured scales. The tips on stalks along contour slopes and valleys will contact the environmental surface if a) the contour interdigitates with a permanent irregularity of the substrate, or b) the substrate molds to the scale contour. But given scale relief an order of magnitude greater than the maximum observed stalk length, "finding" the substrate does not depend on stalk length. Possibly the fine structure of contoured scales is not selected to "find" the substrate as setae do, but to interact with particular portions of the substrate which "find" the stalks by offering resistance or purchase to the scale contours. Short stalks, regardless of the associated tip shape, may be functionally advantageous on multicarinate scales if, by "roughening" the keel slopes, the stalks increase the frictional coefficient of the scale surface.

2) Although the variation in tip shape is continuous, there are two basic and numerically dominant shapes, the hook and spatula (Fig. 21). The hook tip on spines and spikes (and even prongs) functions like a microscopic hook to engage irregularities of the environmental surface (see above and Hiller, 1968). There is a variety of hypotheses on spatular mechanisms (see Russell, 1975 and Hiller, 1968 for review), but two seem most likely for anoles. Compression and lateral expansion of the hook tip into a spatula could be an adaptation a) to shift from a prehensile mechanism to an adhesive one (Hiller, 1968 for geckos), or b) to add the option of an adhesive mechanism to the existing prehension. In either case, the difference between the hook and the spatula seems to be adhesion. An adhesive gripping force depends a) on the surface energy or tension of the environmental surface and of the seta keratin, and b) on the area of contact between them. Given that the seta keratin itself is preadapted for adhesion, selection might increase the area of contact of the tip in the following sequence (Fig. 21): a) reduction in the stalk taper to yield a thicker, larger tip—the prong, b) compression of the round or oval prong to form a planar surface and increase the effective area—the seta-prong, and c) expansion of the flattened surface—the seta. The prong and seta-prong shapes are very rare in generalized anoles (Fig. 23) and appear to represent developmental and evolutionary transitions linking the hook and the spatula.

There is no direct evidence for an adhesive nor for a prehensile mechanism in anoles. Hiller (1968) argues strongly for an adhesion mechanism based on the morphology of the spatula and on experiments measuring the clinging force of geckos on a series of artificial surfaces. The force required to dislodge a gecko from a horizontal surface was directly proportional to the surface tension of the material (Hiller, 1968). Considerable force was required to dislodge the animal from glass which has high surface tension (contact angle of water droplet with glass is 0°), while the animal had little or no adhesive strength on certain plastics of low surface tension (water-drop contact angles of 80° or more). Hiller (1968) argues that "velcro"-like prehensile mechanisms can be excluded because a) roughening the surface of a low surface tension material results in only a slight increase in gripping force, and b) pulling the animal perpendicular rather than parallel to low ridges on the unroughened surface of a low surface tension material

resulted in only a slight increase in gripping force (values were not reported in either case). In Hiller's adhesion hypothesis whole animal adherence occurs as the spatula is brought into intimate contact with a flat, high surface tension substrate. Surface roughness or ultramicroscopic irregularities will interfere with this process so that the animal is unable to cling to such surfaces without its claws. Russell (1976) augments Hiller's argument with the hypothesis that the waxy secretions on leaves and smooth bark provide the initial advantage to seta-bearing geckos.

There are two major difficulties in accepting or extending the adhesion hypotheses to anoles. 1) The surface properties of vegetation suggest that, if an adhesive mechanism alone is possible, anoles could not use some of the substrates they clearly thrive on. The majority of plant surfaces appear to have lower surface tension than Hiller (1968) found was required in geckos (contact angles of 80° or less were required for even modest adhesive force). The common chemical constituents of plant waxes have (water drop) contact angles from 94°–108°; the isolated smooth surfaces of the native waxes yield angles between 80° and 108° (Martin and Juniper, 1970). The accumulated SEM data on leaf and stem surfaces (see review in Martin and Juniper, 1970) indicate that the surfaces are also highly irregular and rough in the dimensional scale of the spatulae: waxes commonly exist in projecting rods or semicrystalline excrescences; the epidermis may be grooved or the individual cells convex or granular; trichomes often project from the surface of leaves; stems and twigs have cracks, ridges, rough scars, and considerable debris. Only a portion, and often a small portion (e.g., 28% on corn leaves, Martin and Juniper, 1970), of the leaf or bark area is flat and smooth enough to make close and complete contact with the spatula. Fine structural irregularity raises the contact angle of many surfaces to better than 110°; in Holloway's (1969) study of the leaf surfaces of 40 common plant species, 24 have contact angles greater than 110°, and an additional 6 have contact angles between 90° and 110°. Presumably the small size and active application of setae will permit the spatulae to "find" the smooth portions of the surface better than a water droplet which rides on the peaks of the irregularities, so that the contact angles in excess of 110° may not themselves be relevant. But, major portions of common vegetational surfaces (leaves, young bark, stems, and particularly grass blades) are unsuitable for adhesion. They have been selected for surface irregularity and low surface tension to inhibit the adhesion of water droplets (Martin and Juniper, 1970). 2) There is little indication that anoles in natural habitats are selecting particular plant species or surfaces which might have high surface tension and low surface irregularity (but see Kiester *et al.*, 1975 for *auratus*). In the laboratory, anoles will adhere to smooth, high surface tension glass and waxy, low surface tension leaves (neither surface will accept the claw). The discrepancy among Hiller's findings, the properties of natural surfaces, and the behavior of anoles need to be addressed directly with adhesive force experiments on natural surfaces, but provisionally we would suggest that spatular morphology permits coexisting adhesion and prehension mechanisms. The eccentric attachment of the spatula to the stalk and the broad leading margin could permit the setae to function as a hook. It seems to us possible that the foot and lamellar movements wipe the spatulae over the environmental surface until the leading edge of the spatula catches on a wax rod/crystal or cuticular irregularity or until the spatular surface finds a smooth, high surface tension area of cuticle. Either would establish the grip and, since most leaf and twig surfaces are rough/smooth mosaics, even adjacent setae might exhibit different gripping

mechanisms. Anole setae probably represent an adaptation for this mosaic surface structure and a variety of surface tensions.

IMPLICATIONS FOR THE "RETROGRADE" SERIES

This general discussion of the spine-seta series provides a context within which to evaluate the trends in the *annectens-onca* and *auratus* lineages. The two lines offer an extraordinary contrast, not in the morphology of members of the series, for all but *onca* have quite similar representatives of all stages, but in specialization for long or short stalks and for hook or spatulate tips. In generalized anoles the subdigital surface is covered with spatulate and hook tips in about the proportions 60/40 or 70/30, depending on body size and ecomorph. In *auratus* the series is shifted even further toward the spatula and relatively long stalks. All the subdigital scales bear setae, and spines are quite rare. In the *annectens-onca* line, the series is shifted in the opposite direction, until in adult *onca* only spines are present. The functional significance of this divergence is at least in part related to the substrate features.

A. auratus and Grass Surfaces

The characteristic substrates of *auratus*, grass blades, sheaths, and stems (culms), will not accept the claw, and most of the surface irregularities are too small for scale contouring to be effective. Purchase largely, if not entirely, depends on adaptations of the spine-seta series. Substrate selection should favor long stalks to permit the tips to "find" the surface, since grass is too rigid to comply and "find" the tips, and either a hook (spike) or spatulate (seta) tip, depending on surface tension and irregularity. The surface characteristics of the Panamanian grasses are not known, but the available data suggest that most Graminaceae have a) ribs or keels on stems, sheaths, and blades, b) prominent surface corrugations or groove/ridge contours between the ribs on the blades, c) trichomes, and d) a coating of surface wax (Martin and Juniper, 1970; Challen, 1960; personal observation). Challen (1960) found contact angles of 135° and 110° on two temperate grasses (*Agropyron repens* and *Festuca pratensis*). Removing the surface wax reduced the angles to about 67° and 77°, respectively (Challen, 1960). The common Panamanian grasses (*Paniculum pilosum*, *Paspalum conjugatum*, and *P. paniculatum;* Croat, 1978) probably used by *auratus* have surface ribs and corrugations at least as prominent as those of the species investigated by Challen (1960). The surfaces *auratus* uses are clearly "rough" in the dimensional scale of the tips and probably have a relatively low surface tension. Systematic descriptions, however, indicate regional variation in some of the sources of surface roughness (e.g., the stem may lack trichomes while the sheath or blades are pubescent; Croat, 1978). Although a non-adhesive mechanism appears to be required and dominant, there is sufficient variation among the regions of the grass plant and on an ultrastructural level (e.g., smooth, moderate surface tension cuticle exposed between wax crystals and adjacent to the ribs) to permit the possibility of supplemental or occasional adhesive contacts. If these adhesive contacts are behaviorally significant and if anole setae can function in either prehension or adhesion, selection related to grass substrates would favor setae or a combination of setae and tall spikes. The West Indian grass anole, *A. pulchellus*, exhibits the second condition: setae and large numbers of spikes occur on a well-developed pad. In *auratus*, the seta spatula is somewhat narrower, but setae cover almost all of the subdigital surface. The distribution of setae to all phalanges is apparently correlated with the absence of an expanded phalanx ii pad and with dimensions and density parameters within the spike to

seta series (see discussion of lamellar scale shape). The *auratus* morphology represents adaptation for the use of grass or grossly smooth vegetational surfaces and for a narrow pad region. The differences between *auratus* and *pulchellus* in pad width and in the specialization for setae versus the combination of spikes and setae are major, but we cannot yet interpret their functional significance. It does seem reasonably clear, however, that if the environmental surface is grossly smooth, and fine structure is responsible for whole animal adherence, setae or the spike-seta portion of the morphotypic series is selectively advantageous.

A. *onca* and Diminished Selection for Setae

While *onca* (and presumably *annectens*) climb, setae would not necessarily be appropriate or advantageous, given the climbing behavior and vegetation (see Williams, 1974; Collins, 1971). The vegetation in *onca* habitat is unusual for an anole; there are no broad leaf plants and few trees. Fence posts and the dense maze of thorn scrub bushes are readily negotiated with claws. The thorn scrub branches are used in combination (two or more perches support the animal) so that foot positions can be chosen to take advantage of the claws and even opposing combinations of digits. *Dipsosaurus*, a predominantly terrestrial iguanid that also clambers into sage and other scrub bushes, exhibits very similar "climbing" behavior. In captivity *onca* climb bark and apparently "rough" surfaces and "walk" through a closely spaced mesh of small diameter perches as well as any other anole. If *onca* are placed in a generalized anole habitat—the more open, arboreal network of perches or a trunk-ground interface—they do not seem to display the repertoire of fast acrobatic and single perch maneuvers which most other anoles have. When the distance between perches is greater than a comfortable step or a short hop, they usually drop from the perch rather than leaping. Although the scrub bush is superficially like the arboreal habitat where anoles obviously depend on seta/pad function, the mesh of perches is dense relative to adult *onca* body size, and there is a meter or more distance between bushes. These factors effectively preclude the single perch and fast acrobatic behavioral strategies of generalized trunk-ground anoles. The vegetational structure permits *onca* (and *Dipsosaurus*) to use climbing behaviors that require precise foot placement but are not otherwise very different from those used in terrestrial locomotion. Given the character of the vegetational/structural habitat and the behavioral strategies of anoles, it is likely that habitat selection for seta/pad function is diminished in adult *onca*.

Juvenile *onca* are found in thorn bushes and the dense dry grass at the base of the bush (K. Miyata, personal communication). Sandy areas surrounding the thorn bush islands seem to be rarely encountered, and this could reduce the selection for multicarinate features in hatchlings. Also, the body size range over which the juvenile morphology occurs is about half that of the adult (Maderson and Williams, in preparation), so that the relationship between body size and perch/perch matrix dimensions is more like that of a grass anole than that of adult *onca*. It is not known whether juvenile *onca* utilize the behavioral strategies of generalized grass or trunk-ground anoles, but it seems feasible for juveniles to perch on a single twig, grass blade, or thorn bush leaf while it does not seem feasible for the adults. The surface properties of these substrates might permit adhesion, so that it is not clear that the advantage of setae would be diminished for the juvenile to the same degree as it appears to be for the adult. But, grass, twigs, and probably the available leaf surfaces would almost certainly provide microscopically rough substrates which would be engaged by

the prehensile elements of the fine structural series (prong/spike/spine). Robust keels like those of the adult would probably be less effective in dealing with this range of substrates than setae or the prehensile forms in the fine structural series.

Juvenile *onca* morphology underlines the argument that diminished selection for setae is not by itself an adequate argument for the substitution of multicarinate scales and the convergence toward sand-dwelling iguanids demonstrated by the adult *onca* morphology. If lamellae and setae are developmentally expensive (Williams, 1974) and not particularly advantageous in locomotion, it is naively reasonable to expect the substitution of spine/spike-covered generalized subdigital scales like those in the phalanx iii region of many anoles or in juvenile *onca* or in some of the para-anoline genera (Peterson and Williams, in preparation). A number of semiaquatic, streamside anole species retain the pad and gross characters of generalized anoles, but spikes and prongs have completely replaced setae on the subdigital scales (Peterson and Williams, in preparation).

Adult *onca* morphology reflects a parallel but more extreme "retrograde" shift in the spine-seta series coupled with a trend to contour the scales. It appears that this is related to the combination of sand and bark substrates. The surface irregularity which dominates bark or must be created in sand is at least an order of magnitude larger than that on grass blades. Purchase and traction on bark and sand depend on adaptations—claws, scale shape, and keels—at a larger dimensional scale than spikes and setae. The subdigital surface may be selected for short stalks and hook tips to increase the frictional coefficient of the keel slopes or even to contribute some grip by prehension, but much of the propulsive force is probably transmitted independent of the spines.

The comparatively reduced significance of the spine-seta series in actual grip may be indicated by the *onca* spine morphology itself. Except where the spines are associated with a contour, as on a hillock or adjacent to a keel, their height and diameter are less than those of generalized subdigital spines. With a diameter of 0.3–0.45 μ and a density of 1.2 spines/sq μ, most of the scale surface is bare. By itself, the reduced size of the spines suggests a simple retrograde shift toward Oberhautchen spinules, but the combination of low spine density and small individual spines appears to indicate a general trend toward repression of the spine-seta series and a completely bare contoured surface similar to that of multicarinate scales in some iguanids, e.g., *Dipsosaurus*.

A. annectens and Juvenile *onca* as Alternative Models for the "Retrograde" Series

The earlier paper outlined a five-stage sequence in the "retrograde" evolution from the typical anoline pad morphology to the keeled subdigital surface in *annectens* and *onca* (Williams, 1974). Through the first three steps—narrowing of the lamellae, reduction in the number of lamellae, and loss of the raised character of the pad—the pad dedifferentiates from the adjacent phalanx i and iii scales. If phalangeal length is constant, narrowing of the pad and reduction in the number of scales convert the lamellar scale shape into that of generalized subdigital scales. Pad dedifferentiation characterizes a variety of "Norops" species, including *auratus*, and is approached by *A. chrysolepis*. The fourth and fifth steps in the sequence comprise the shift from generalized subdigital scales to multicarinate scales. Keels are introduced into the phalanx iii series in *annectens* (step four), and in *onca* the entire series of subdigital scales is multicarinate (step five).

The additional comparisons and fine structural data alter our view of the sequence in several ways. 1) It is no longer

clear that *auratus*, as an example of a "Norops" species, is an appropriate model for the early stages in the sequence. The expanded seta distribution in *auratus* demonstrates that dedifferentiation of the pad is not necessarily linked to a decrease in the seta-bearing area nor to the substitution of multicarinate scales. 2) There appear to be two alternative sequences.

If juvenile *onca* morphology is used to model the intermediate stages, the sequence might a) begin with a trunk-ground or even more probably a grass anole with gross morphology similar to that of *auratus*, b) progress by more extreme dedifferentiation of the pad region (including loss of the frayed lamellar border and extreme narrowing of the lamellae) combined with the replacement of setae by spikes, prongs, and spines to yield the gross morphology of the *onca* juvenile, and c) culminate with keels and marked contour features throughout the series of subdigital scales (the *onca* condition). In this scheme *A. annectens* would represent a parallel lineage independent of that of *onca* after the first step in the sequence.

If, on the other hand, *A. annectens* morphology is considered representative of the intermediate stages, the "retrograde" sequence could a) begin with a trunk-ground anole (broadly defined) not unlike *A. chrysolepis*, i.e., perhaps with narrow lamellae, but a defined pad region and a few phalanx i keels, b) continue with elaboration of the keel features in the phalanx i region (the *A. whitemani* variant morphology), c) follow this by invasion of keels into the phalanx iii region of generalized subdigital scales (the *A. annectens* morphology), and d) finally substitute multicarinate scales for lamellae and setae in the phalanx ii region (the *onca* condition). In this scheme the "Norops" condition may arise at any point before the substitution of keels for lamellae and setae in the phalanx ii region, and the juvenile *onca* morphology would be considered an ontogenetic adaptation with no relationship to the phylogeny of adult morphology.

The critical difference between these sequences is whether the adhesive pad dedifferentiates prior to the appearance of multicarinate scales or whether multicarinate scales progressively encroach on and replace lamellae. These different modes of origin for the multicarinate scales correspond to two possible models for transitional scales. *Onca* juvenile scales (e.g., scale 13) have the gross shape of the adult multicarinate scales and rounded contours without the bare areas which characterize keels. A "retrograde" shift in the spine to seta series has occurred over most of the scale. The central portion has prongs, a "more conservative" morphology than the spikes. The latter occur distally and laterally, suggesting that the trend progresses inward from the scale margins. But, on the whole, the scale surface is reasonably homogeneous, and adjacent scales have very similar achitecture.

A. annectens scale 9 suggests a very different mode of evolution in scale architecture. Here the transitional scale shape is close to that of the lamellae, but the distal margin is robust and set with bosses or keels. The bosses are set into fields of spines, spikes, prongs, and a few rare setae. The fine structure is extraordinarily heterogeneous, apart from the distal border which is covered with spines. Compared to the morphology of scales in the *onca* hatchlings, the fine structure of scale 9 appears chaotic and disrupted. Scale 9 is also markedly different from the lamellae and multicarinate scales on either side of it. The small keels which are present on the lamellae appear to become progressively more robust toward the interphalangeal joints (at scales 9 and 15). The morphology itself suggests that the transition begins as keels invade the surface of lamellae.

It is not clear which of these two sequences or models of the transitional

morphology are correct. We cannot provide incisive arguments for or against either of them, but the second or *A. annectens* model seems somewhat more plausible.

1) If *onca* and *annectens* represent parallel lineages which have been independent from the *chrysolepis*-like stage of the sequence, it is difficult to explain the close resemblance in non-digital characters (Williams, 1974). There are marked differences in digital characters (e.g., phalangeal length, scale shape, keel placement, and the retention of lamellae and setae), but these could represent adaptation to somewhat different structural habitats.

2) Each of the model intermediates has equivocal status or relevance to the evolution of *onca*. *A. annectens* is a unique specimen which closely resembles *onca* in non-digital characters. There is the possibility it is an individual variant of *onca*. Elements of the morphology might be relevant to the sequence in this event, but the particular combination of characters on which the sequence is based could as readily reflect developmental patterns as the phylogenetic sequence. The juvenile *onca* morphology may, on the other hand, imply the phylogenetic sequence or reflect ontogenetic adaptation for a smaller body size and different habitat and behavior. There are two critical features on which the juvenile morphology makes any claim as an intermediate between generalized anoles and *onca:* the absence of definite keels and the presence of spikes and prongs. The absence of definite keels on the subdigital scales in the hatchling of another anole species (*A. cristatellus*) suggests that this character is not restricted to *onca* juveniles. It may be a feature of juvenile anoles and an ontogenetic adaptation which coincidentally parallels the phylogenetic sequence. The presence of well-developed contours usually in the position of the adult keels and on all the subdigital scales also suggests a very derived status in terms of keel elaboration. Juvenile *cristatellus* have setae and the same fine structural series as the adults, but with decreased stalk height. The opposite difference—increased stalk height—in the juvenile *onca* appears to be a feature that is unique to *onca* juveniles. If the *onca* juvenile morphology is converted into a hypothetical adult by the addition of bare areas to the contours to form keels, the result is a form which is very similar to *onca* and an apparently later member of the transitional series than *annectens*. If the hypothetical adult/juvenile *onca* is used as the basis of a revised "retrograde" sequence, it suggests very little about the early stages of the lineage, particularly about keel origin and expansion, so that a number of sequences are possible, including the early part of the *annectens* sequence. Any of the juvenile *onca* sequences and the *annectens* sequence differ markedly on the issue of a sequential versus a simultaneous shift to multicarinate scales in the phalanx ii and iii regions. Even the hypothetical adult version of the juvenile *onca* morphology still leaves the two model intermediates as mutually exclusive forms in the *onca* lineage.

3) The alternative sequences and models for transitional scale types can also be compared in terms of circumstantial support from the comparative data.

a) The pattern of transitional scales based on the *onca* juvenile morphology has some comparative support although it is unique in most features. In the *lionotus* species group there is a general trend to replace setae with spikes, and on several lamellae in *A. lionotus* only the central portion of the scale has setae while the surrounding areas are covered with spikes. The "retrograde" shift in fine structure appears to occur from the lateral and distal portions of the scale inward, but, in this case, the shift occurs on a lamellar scale and there are no contours present. The *annectens* scale 9 fine structure is to our knowledge unique, but

apart from *annectens*, there are no examples of keels invading lamellae. Given that keels are being added to the scale surface, the disrupted, heterogeneous fine structure is no less plausible than the more homogeneous fine structure of the *onca* juvenile.

b) The transitional scale model and sequence based on the *onca* juvenile are unusual for anoles because they imply so little regional differentiation and sequential change. The "retrograde" shift from setae to spikes in *A. lionotus* appears to have occurred in a scale-by-scale sequence beginning at the i/ii and ii/iii interphalangeal joints and progressing toward the center of the pad. This is similar to the suggested pattern of keel encroachment in *annectens* and is markedly different from the simultaneous change in two or more phalangeal regions suggested by juvenile *onca*. The expansion or retraction of setae in the phalanx ii region (the phalanx iii and iv regions of the fourth toe) of West Indian anoles also appears to occur with a sequential scale-by-scale pattern. Marked differentiation in fine structure of the phalanx i and ii regions occurs even in some extreme "Norops" species like *A. aequatorialis*, *A. notopholis*, and *A. meridionalis*. The dominant morphological and evolutionary patterns within the genus are regional differentiation and sequential change (scale-by-scale and phalangeal region-by-phalangeal region). Clearly the *onca* lineage could be exceptional in this regard, but the sequence and transitional morphology implied by *annectens* is quite consistent with the patterns we have encountered elsewhere in the genus while those suggested by the *onca* juvenile are not.

c) There is no great difficulty in deriving *A. annectens* from generalized trunk-ground forms such as *A. chrysolepis*, and parallels for the early stages in the sequence can be found among other lineages (e.g., *A. whitemani*). But it is very difficult to find a model ancestor for the juvenile *onca* morphology. All of the prospective models with which we are familiar (e.g., *A. chrysolepis*, *A. barkeri*, *A. notopholis*, *A. tropidonotus*, *A. auratus*, *A. nebulosus*) have keels or bare areas. Based on the morphology of these more generalized related species, either keels and bare areas are lost in the early portion of the *onca* juvenile sequence and then "re-acquired" at the *onca* stage or the absence of bare areas is not descriptive of the phylogenetic intermediate. If one accepts, as is argued above, that the absence of bare areas on the contours is an ontogenetic adaptation and that the adult intermediate morphology includes keels, then any of the forms cited above could model the starting point of the *onca* lineage. The gap between any of the prospective initial morphologies and that of juvenile *onca* is so great that it simply is not clear how the sequence might start. The "Norops" condition is combined with narrow but definite lamellae in *A. notopholis* and *A. tropidonotus*, but there is no evidence of a "retrograde" shift in fine structure or conversion of phalanx ii lamellae into generalized subdigital scales. *A. auratus* exhibits the "Norops" condition, narrow lamellae and poor regional differentiation in fine structure, but the latter is associated with an expansion of setae into the phalanx i region rather than a "retrograde" shift. *A. barkeri* exhibits a "retrograde" shift in the fine structure of the phalanx ii and iii regions (prongs are present), but there is little indication of pad dedifferentiation or replacement of lamellar scales. The differences between generalized anoles and juvenile *onca* suggest that three trends occurred in the intervening stages: dedifferentiation of the pad and lamellae, a "retrograde" shift in the fine structure, and expansion of contours and keels into the phalanx ii and iii regions. But there is no real indication of the order or relative emphasis of these

trends during the early portion of the radiation.

Summary: The relative efficacy of the *annectens* and juvenile *onca* specimens as phylogenetic models for the *onca* lineage cannot be evaluated with any degree of security from the available data. The possibility that *annectens* is an aberrant version of *onca* or represents an independent radiation has to be weighed against the possibility that the differences between *onca* juveniles and adults coincidentally parallel the phylogenetic sequence. But the odds appear to be shifted slightly in favor of *annectens* as a model. 1) The similarity between *annectens* and *onca* in non-digital characters is so great that it seems unlikely that they represent as distantly related forms as the *onca* juvenile morphology would imply. 2) The individual variation we usually encounter (e.g., *whitemani*) involves a single morphological series, while that in *annectens* involves all three series plus scale number and phalangeal lengths. *A. annectens* is thus less likely to be an individual variant than if pad retention were the only character distinguishing it from *onca*. 3) Comparison with the juvenile of another anole species and consideration of the more generalized anoles related to *onca* suggest that the absence of definite keels in juvenile *onca* is an ontogenetic adaptation which coincidentally parallels the phylogenetic sequence. If this is the case, it is only the presence of longer stalks in the fine structural series which makes the case for juvenile *onca* as a model intermediate; the rest of the features are highly derived and resemble adult *onca*. 4) The models for transitional scales based on *annectens* scale 9 and *onca* juvenile scales seem equally plausible. The *annectens* sequence is more consistent with the evolutionary patterns for regional differentiation and sequential change that we have encountered elsewhere in the genus.

CONCLUSIONS

The significant differences in the subdigital morphology of *annectens*, *onca*, *chrysolepis*, and *auratus* can be described in terms of changes in three morphological series: a) scale shape, b) scale surface contouring, and c) fine structure or the spine-seta series. The series are quite similar in the different species, and the dominant evolutionary pattern is change in the distribution or relative abundance of members of the series.

There appear to be two lineages: the *chrysolepis-auratus* lineage and the *chrysolepis-annectens-onca* lineage. An alternative hypothesis is that the latter species are divergent and that the morphology of *onca* juveniles rather than that of *annectens* is the relevant model for the evolution of adult *onca* morphology.

In the *auratus* lineage there are trends for: a) pad dedifferentiation, b) limited keel elaboration in the lateral portion of the phalanx i scales, and c) expansion of seta distribution to cover not only the pad scales, but also the entire phalanx i region. In the *annectens-onca* lineage there are trends for: a) pad dedifferentiation, b) expansion in the distribution and increased size and number of keels, and c) a "retrograde" shift from setae to spines in the pad region. The combination of these trends results in the progressive substitution of multicarinate scales for lamellae and for smooth generalized subdigital scales. In *onca* this substitution has been complete. In *annectens* it has occurred in the phalanx i and iii regions and begun in the phalanx ii area, but setae and lamellae are still present.

Dedifferentiation of the pad (reduction in lamellar number and width and the absence of a raised distal border [i.e., the "Norops" condition]) occurs in both lineages, but the significance of the trend is probably different in each case. In *au-*

ratus pad dedifferentiation is associated with the expansion of setae into the phalanx i region. The seta-bearing area which is "lost" through decreased lamellar width is more than compensated for by the increased phalangeal length and expansion of setae onto the non-lamellar phalanx i scales. There is no indication that pad dedifferentiation in *auratus* is associated with decreased competence of the setae for gripping or with selection for another mechanism. In contrast, pad dedifferentiation in the *annectens-onca* lineage is associated with reduction in the seta-bearing area (relative to body size). Almost certainly, the competence of the fine structural series in maintaining grip is compromised relative to generalized anoles.

In the *annectens-onca* lineage the substitution of keels and a highly contoured scale surface for lamellae and setae appears to reflect selection for an alternative "gripping" or "traction" device. Keels probably function as "traction" devices and presumably are more effective than the fine structural series on surfaces with gross irregularity, like most mature bark, or on surfaces with low cohesion of particles, like loose sand or dirt. Within *Anolis* subdigital keels occur in the phalanx i region of species which use the trunk-ground structural niche (broadly defined) and are rare in other ecomorphs. In at least one case keels are elaborated in a trunk-ground species which has invaded habitat similar to that of *onca*. Limited comparisons among non-anole iguanids suggest that locomotion on loose sand or dirt selects for additional and larger keels. The comparative data suggest that the *annectens-onca* lineage represents a radiation of trunk-ground anoles into extreme xeric habitats where there is enhanced selection for keels and "traction" devices which are effective on the combination of bark and loose sand (see also below).

The fine structural series includes a number of morphotypes which act like microscopic hooks in addition to setae which may alternate this prehensile mechanism with adhesion. The fine structural series is adapted to utilize a) microscopic surface irregularity, or b) high surface tension, smooth regions of a grossly smooth environmental surface like that of leaves, stems, and twigs. The trend to increase the distribution and to emphasize the fine structural series in *auratus* correlates with behavioral specialization for perching and acrobatics on single grass blades, stems, and twigs on which robust keels like those of *onca* would provide too little contact between the subdigital and environmental surfaces.

The extreme xeric habitats of *onca* offer relatively little broad leaf and grossly smooth vegetation which can be used by an animal with adult *onca* body size. Given the body size of adult *onca*, the dense maze of small diameter thorn bush twigs precludes most of the single perch and fast acrobatic behavioral strategies which select for pad function in *auratus* and generalized anoles. The character of the vegetation in *onca* habitat is such that selection for "grip" based on the fine structural series is probably diminished.

Several alternative sequences of evolutionary morphological paths toward *annectens* and *onca* are discussed. The most likely sequence, in our judgment, begins with a generalized trunk-ground form, which, like *chrysolepis*, has a narrow pad and a few keels in the phalanx i region. Radiation into a more xeric habitat in which bare soil and sand becomes the common terrestrial component of the trunk-ground structural habitat, but in which trees and large open shrubs are still present, would select for the elaboration of the keels in the phalanx i region (the variant *A. whitemani* morphology) and perhaps expansion of keeled scales into the phalanx iii region (the *annectens* morphology). Finally, multicarinate scales replace lamellae and setae in the phalanx ii region (the *onca* morphology). The

complete substitution of multicarinate scales seems to be associated with the invasion of extreme xeric habitats a) where vegetation is scarce and selection for locomotion on loose sand is even more enhanced, and b) where the residual vegetation does not offer enough smooth surfaces nor select for behaviors which would maintain the setae and spike portions of the fine structural series.

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The American Orb-Weaver Genera *Dolichognatha* and *Tetragnatha* North of Mexico (Araneae: Araneidae, Tetragnathinae)

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THE AMERICAN ORB-WEAVER GENERA *DOLICHOGNATHA* AND *TETRAGNATHA* NORTH OF MEXICO (ARANEAE: ARANEIDAE, TETRAGNATHINAE)

HERBERT W. LEVI[1]

ABSTRACT. One species of *Dolichognatha* and fifteen species of *Tetragnatha* are found in North America north of Mexico. Of these, three are new: *T. earnra* from the Everglades; *T. shoshone*, widespread in south central Canadian provinces and north central states; and *T. branda*, found from Connecticut to Mississippi.

Tetragnatha harrodi is a synonym of *T. dearmata*, described from northern Eurasia. *Tetragnatha antillana* is a synonym of the cosmotropical *T. nitens*.

Males of *Tetragnatha* are readily separated by the shape and structure of the palpal conductor and paracymbium; they cannot be separated by the structure of the chelicerae. Females can be separated by the configuration and placement of seminal receptacles, as revealed by simple dissection; they cannot be separated by the structure of the chelicerae.

Several *Tetragnatha* species are distributed from Canada to the tropics. Several uncommon species probably have specialized habitats: *T. viridis* in pines; *T. vermiformis* on reeds; and *T. branda* in salt marsh grass.

INTRODUCTION

One of the aims of a generic revision is to find diagnostic characters that separate the species. Reliable identification is essential for any work by ecologists and physiologists. Another aim, of course, is to reveal the relationships among the species, and, more important, the relationship of the genus to other genera.

Tetragnatha species are among the most abundant spiders worldwide. North American species can be determined only with difficulty using Chickering's papers (1957a, b, c, 1959). Chickering (with one exception) determined species correctly, but could determine only males; his drawings are awkward, often failing to tell what position is illustrated or whether the structure illustrated is from the left or right palpus. Also, his *Tetragnatha* reports are limited geographically to Michigan and to some tropical American regions. *Tetragnatha* is the second largest araneid genus north of Mexico, after *Araneus*.

Despite a conscious effort not to change names, two synonymies had to be resolved. To avoid further name changes, neotypes were designated for several old names, the use of which has been based mainly on tradition rather than on the type method. The neotypes were designated in accordance with Article 75 (1961) of the International Code of Zoological Nomenclature.

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The American Museum of Natural History provided about 4000 vials of common *Tetragnatha* species; the Museum of Comparative Zoology between 2000 and 2500 vials; the Canadian National Collections 600 vials; the Florida State Collection of Arthropods and the Exline-Peck collection about 300 vials each.

Mapping, rewriting, and typing were done by Cecile Villars; some rewriting was done by L. R. Levi. John Hunter and Edward Seling made the scanning electron micrographs.

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METHODS OF STUDY

1. *Background.* Washed sand is the ideal surface on which to examine the long-legged *Tetragnatha* in various views. The palpus does not usually have to be removed to reveal its diagnostic features; however, magnification of at least 50 to 80 times is required to examine the shape of the tip of the conductor.

2. *Seminal Receptacles.* To determine females it is necessary to examine the seminal receptacles. At first this was done by removing the genital area and clearing it in clove oil or mounting it on a slide: the cleared genital area has been illustrated for all species. Because of their large size, it is more difficult and time-consuming to clear the whole spider.

An easier method is to lift the exoskeleton of the genital operculum, carefully separating it from clinging tissues, and search for the lightly sclerotized seminal receptacles. Most species can readily be determined by the position and shape of the seminal receptacles (together with eye placement).

To lift the genital cover, cut with a mounted and sharpened minutenadel, starting from the anterior corner between the book-lung spiracle and the genital cover, cutting in a posterior direction toward the genital opening. After cutting, carefully lift the exoskeleton and remove tissue clinging to it. Fold the cover back and probe for the seminal receptacles in the tissues adjacent to the cut. Some practice is necessary. Many *Tetragnatha* species are sufficiently common so that a few specimens can be sacrificed for the purpose. While penultimate female specimens may have an indistinct genital cover, the seminal receptacles are not present.

The final method used was to peel the genital cover to the side, place the whole spider in clove oil, and watch the genital area clearing: the area between the seminal receptacles clears first; later the tissue around the more dorsal median receptacle. (The spider should then be removed and the oil washed out in alcohol.)

3. *Eye Distance.* The distance between anterior and posterior lateral eyes is variable. Nevertheless, the relative distance between the two lateral and the two median eyes is consistent and useful. It is best seen from the side with the specimen lodged in sand. The distances were measured from the center of the eye.

4. *Chelicerae.* I first tried to study the genus by illustrating the chelicerae of males and females of various species. But I could not consistently separate species using the shape and number of cheliceral teeth in the fang groove, the shape of the fang, presence of fang cusps (a hump at point of greatest curvature), or length of the chelicerae. Such characters vary enormously within species (Figs. 83–87). Chickering also found the chelicerae unreliable, and depended on palpi to separate the males. Only one mistake was

found in his many determinations of males: he labeled the rare *T. viridis* as *T. versicolor* in collections. However, Chickering resorted to characters of the chelicerae to determine females, and many of these determinations were wrong. The teeth and chelicerae are useful nevertheless in limited ways: male *T. dearmata* and *T. pallescens* always lack the first, distal, long tooth; *T. elongata* generally has longer chelicerae than *T. versicolor*.

Some authors have determined immature North American specimens on the basis of the cheliceral teeth, burdening students of the genus with much questionable reporting. To elevate chelicerae to a reliable character, it would be necessary to raise the inhabitants of egg-sacs of different species and study the allometric growth and development of their chelicerae and teeth. *Tetragnatha* species, like other Araneidae and many other spiders, mature after a variable number of molts; some mature specimens are twice the size of others. In addition, perhaps due to hormonal influences, the chelicerae of some individuals are more developed than those of others (e.g., *T. elongata*, Fig. 83 and *T. pallescens* from Florida, Figs. 134, 135). Other species have larger chelicerae in southern localities than in northern ones (e.g., *T. elongata*, Figs. 84–87). I judged the previous determinations of immatures doubtful because the identifiers often could not place adult specimens correctly.

5. *Measurements.* Measurements of total length are from the clypeus to the posterior tip of the abdomen. Initially ten to twenty specimens of each species were measured to establish variation; subsequently only extremely large and small individuals were measured. If there was a geographical difference in size, this was noted. Total length is not a good measurement, as it is difficult to repeat, and the measurements are intended only to give a general idea of size range, not as a statistical tool to distinguish between species. Furthermore, the smallest size of mature females is only an estimate; dissection was not always made to demonstrate maturity.

6. *Determination.* In this study, for which perhaps 30,000 to 40,000 specimens were available, I had to take some shortcuts to get data for the revision. I did not determine the contents of all vials, nor could I sort some mixed collections. Usually only a male was selected from the vial and carefully examined and recorded. In collections that consisted only of females, I did not examine a specimen unless it was from a poorly collected area or a less common species was suspected. It is possible to determine adult females, but it is less time-consuming to determine males. Gathering data for this revision had a higher priority than labeling collections.

7. *Dubious Species.* In the past when there was doubt as to the distinctness of species (or genera), I tended to lump them, considering it more parsimonious to lump than to split. However, I am aware that some mistakes have been made. *Araniella* (Levi, 1974) of Europe, for instance, contains a number of species, all with similar genitalia but different habits. Unfortunately, I had examined only a few specimens and failed to consult colleagues who knew the species in the field. Also, the genus *Latrodectus* in the family Theridiidae (Levi, 1959) is now known to contain many species difficult to identify by genitalia. Renewed studies are needed for both.

Similarly, what is considered *Tetragnatha versicolor* here may turn out to be several related species. It is particularly disconcerting that the genitalia of *T. viridis*, certainly a distinct species, are very similar to the genitalia of southeastern *T. versicolor*; *T. viridis* differs by being green or reddish in coloration, in having the lateral eyes as far apart as the medians, and in having unusually long mac-

rosetae on the legs. While the genitalia of *T. viridis* strikingly resemble those of southeastern *T. versicolor*, there is greater genitalic difference between southeastern and western *T. versicolor* (Figs. 104–109), suggesting that there may be other sibling species.

8. *Variation. Tetragnatha* species vary as widely in size as do other Araneidae, some individuals being almost twice as large as others of the same species. Is the variability in size a preadaptation to dwarf males found in various genera of the family? Large and small individuals of the same species have different dentition on the chelicerae; smaller individuals have fewer teeth, and the teeth may be relatively larger than those of larger-sized individuals (Figs. 83–87).

9. *Illustrations.* The conventions of illustrations were followed. The light comes from the upper left. In dorsal view, anterior is placed on top; in side view, anterior is on the left. These conventions were not followed for palpi; they are considered separate structures for ease of visualization.

10. *Scanning Electron Micrographs.* Scanning electron micrographs (SEM) were made of conductors and their tips after the illustrations had been completed. It was hoped the SEM would add details for the diagnostic features. While the photographs added these details (Plates 5–7), drying the palpi prior to SEM twisted the soft pleats of tissue and gave the structures a greater curvature; some tips were turned. The drawings were only touched up after examining the photographs; they were not changed. It appears that scanning electron micrographs alone are not a substitute for illustrations made under a dissecting microscope, but are a valuable additional tool.

PHYLOGENETIC CONSIDERATIONS

1. *Tetragnatha.* Tetragnathids are not primitive spiders, various contrary published opinions notwithstanding. The following characters, some shared with species of other genera, are evidence of specialization: the palpus has a separate paracymbium (also in *Pachygnatha* and Linyphiidae); there is no tapetum in the secondary eyes (*Dolichognatha* and *Azilia* share this feature; *Pachygnatha* lacks tapetum only in the posterior median eyes); the lateral eyes are often separated (also in *Azilia*); the chelicerae are modified as holdfasts for mating (also in *Pachygnatha*, *Dolichognatha*, and perhaps other genera); the endites are elongate and widened distally (also in *Pachygnatha*); and when resting, the femoral-patellar joint is straight (Plates 3, 4) (also in most relatives and in Metinae, but not in *Dolichognatha* [Plate 1]).

Primitive features include: the relatively long-lived males; the lack of an embolus cap on the male palpus, allowing males to mate several times; and, perhaps, the use of both palpi simultaneously in sperm induction.

The female genitalia are referred to repeatedly in the literature as haplogyne and primitive. The absence of an epigynum (separate copulating pore) is almost certainly adaptive and specialized. The strong coupling of male and female chelicerae when mating obviates the need for another coupling guide. When mating, the male's venter faces that of the female, and the female's genital opening is directly underneath the male's palpus. The female can curl her abdomen to facilitate the insertion of the embolus (Plate 4).

The median "seminal receptacle" of the female genitalia is almost certainly not that. Wiehle (1967) could not find sperm in this structure, nor does the shape of this structure suggest a sperm storage function. I think it was Stefan Heimer (in correspondence) who suggested that it might be a holdfast for the tip of the conductor. Evidence for this is seen in the shape of the conductor. In those species in which the conductor tip is a large hook, there is little or no me-

dian structure (*viridis, laboriosa, pallescens, caudata, vermiformis*). Species in which the conductor tip is a knob have a spherical median structure (*guatemalensis, elongata, straminea, vermiformis, nitens*). In one species the conductor tip is filiform; here the structure is elongate, apparently matching the filiform tip (*dearmata*, Fig. 83). Perhaps the primitive, haplogyne median seminal receptacle is homologous and was a preadaptation for this structure. To verify these ideas it will be necessary to preserve mating individuals and examine the inserted palpi.

2. *Glenognatha* and *Pachygnatha*. The presence (or absence) of an elaborate tracheal system is of minor phylogenetic importance, and may reflect small size and large surface, or may be an adaptation against water loss in a more arid environment. With a more elaborate and functional tracheal system, the posterior tracheal spiracle moves to an anterior position in *Glenognatha* (as well as in other groups, e.g., some *Dipoena* species and Anyphaenidae). Tracheae are well known to be plastic and adaptive characters, and developed as a result of need (Levi, 1967). The distribution of tracheae is part of a built-in pattern of body growth. Although this general pattern of growth is fixed, variation in detail can be influenced by local need. For instance, by implanting glands that have a high oxygen requirement, it has been demonstrated in insects that the demand for oxygen stimulates an exaggerated production and outgrowth of new tracheae and tracheoles which invest and penetrate the implanted organ. The growing tracheal cells seem to be attracted by sites of reduced oxygen tension (Wigglesworth, 1972).

The palpal structures and female genital structures of *Glenognatha* and *Pachygnatha* share several derived characters, synapomorphies, (Levi, 1980a). Most important, in both, as in *Tetragnatha*, the median rhabdom loops fill the posterior median eyes and the canoe-shaped tapetum has been lost. The canoe-shaped tapetum is still present in the lateral eyes of both *Glenognatha* and *Pachygnatha*, but has been lost in the lateral eyes of *Tetragnatha, Dolichognatha*, and *Azilia*.

3. *Uloborids*. Uloborids share a number of characters with *Tetragnatha*: separation of the lateral eyes; loss of tapetum in secondary eyes; presence of trichobothria proximally on the femora; frequent absence of an epigynum (Opell, 1979); and similarities of palpal structure. Most important perhaps is that many uloborids make an orb-web, as do tetragnathids and all Araneidae. Are these shared characters synapomorphies?

The separate lateral eyes may be a synapomorphy; more likely not. This feature is no doubt related to the resting position of the spiders: unlike most Araneidae, *Tetragnatha* (and uloborids) extend the legs when resting (Plates 3, 4) rather than pulling the anterior legs back so the femoral-patellar joint is flexed. With the anterior legs flexed, there is little space to permit lateral vision (Plate 1). In most Araneoidea the lateral eyes touch; their separation in *Tetragnatha* is no doubt a specialization.

Loss of the tapetum, like loss of any structure, is a poor character for combining groups. The loss in *Tetragnatha* indicates a specialization from the *Araneus*-like eye: the loops of rhabdoms to the median side of the canoe-shaped tapetum fill the back of the eye (Figs. 21, 22) and the tapetum is lost. There is no indication, as there is in *Tetragnatha*, that the ancestor of *Uloborus* had a canoe-shaped tapetum. Perhaps rhabdom rows got scrambled and rows will still be found in some members of the family.

The trichobothria on the femora (Fig. 17) may be a second synapomorphy. But perhaps these trichobothria have a specific sensory function, evolved in response to a similar need in uloborids and *Tetragnatha*. I do not know how common femoral trichobothria are in other

spiders, but they are certainly absent in most Araneidae and probably in most Araneoidea.

The absence of the epigynum among *Tetragnatha* is probably related to the coupling of chelicerae when mating. There is no such correspondence in uloborids. Again, loss of a structure is a poor character to relate groups.

The complex orb construction behavior can perhaps be considered a synapomorphy. Several striking points set uloborids apart from Araneoidea, including tetragnathids, and make a close association unlikely: 1) the cribellum, generally considered a primitive structure, has been lost a number of times in spiders that gave up webs in favor of hunting, but it is present in uloborids, as is a calamistrum; 2) the loss of poison glands in the chelicerae (also reported in the unrelated liphistiomorph *Heptathela*) is a very unusual specialization, possible only in spiders that overpower their prey by wrapping in silk; 3) the rhabdom arrangement within the eye is not like that found in Araneoidea (Homann, 1950, 1971); and 4) the important structure of the male palpi is not close to that of Araneoidea generally, although closest to that of *Tetragnatha*. Other unique attributes of uloborids are the hair covering, the individual hairs often being constricted at the base; the elongate labium; and the laterally bulging sternum.

Tetragnatha is close to *Meta*, and spiders related to *Meta* are probably the most primitive Araneoidea, having most plesiomorph characters of the superfamily. The orb-web is present in *Meta* but has been lost in some specialized Araneidae (*Archemorus*, *Mastophora*) and Uloboridae (*Miagrammopes*). The orb-web must be a primitive structure, and the webs of theridiids and linyphiids derived (see also Brignoli, 1979; Levi, 1980b).

Growth and Size. All spider individuals pass through a succession of molts before maturing; the number of molts varies even within a given species. Individuals that undergo fewer molts are smaller in mature size than those that matured after a greater number of molts. The size range is greater among adults of araneid species than in species of other families. Usually in any araneid population some mature individuals are twice the size of others, and there may be large geographical size variation as well. Perhaps such size variations preadapt for the occurrence of dwarf males in various araneid genera. The variability in number of instars of spiders differs from the steady number in most mites and pseudoscorpions.

If individuals mature at various sizes, are the small and large adults proportional or are the adults the result of allometric growth? This knowledge is important not only for those who want to use random numerical methods to differentiate species, but also for those who want to differentiate *Tetragnatha* species by proportions and cheliceral teeth.

Illustrations and measurements were made of a large male *T. elongata* from Texas (Fig. 87), and a small male from Wisconsin (Fig. 85). The total length of the large male was 8.6 mm; the small one, 6.2 mm (72% the total length of the large one). The length of the smaller carapace, as measured on the illustration, was 72% of that of the larger one. The smaller chelicerae measured 60% of the cheliceral length of the larger spider. The length of the palpal tibia-tarsus was 60%, but the smaller palpal bulb was 80% of the larger one, and the length of the conductor was 88%. The seminal receptacles of a large Texas female are slightly smaller than those of a smaller female from Massachusetts. But more important is that the chelicerae and their teeth, commonly used to differentiate *Tetragnatha* species, differ widely. (The left chelicera pictured in Figure 85 had two teeth next to each other, but this condition was not present on the right chelicera of the same individual.) While the large individuals of *T. elongata* had many more cheliceral teeth

than did the small individuals, the most characteristic teeth as well as the spur were present in both sizes. Of great interest are relative changes in proportions of the palpal cymbium. Does the cymbium correspond more with leg length than with that of the palpal bulb? The cymbium of the large Texas specimen extends beyond the tip of the conductor (Fig. 87); that of the small Wisconsin individual is shorter than the conductor (Fig. 85).

To summarize, growth is allometric, and the genitalia of larger and smaller individuals are more alike than other body parts. Random measurements might generally separate size classes and are not so useful as the study of genitalia for the separation of species. Also, the chelicerae are not as diagnostic as the genitalia. Seeley's study (1928), which revised North American *Tetragnatha* using mainly the armature of the chelicerae, is only of limited use. Chickering's publication on the *Tetragnatha* of Michigan (1959), and those of Mexico, Central America, and Jamaica (1957a,b,c and 1962), used mainly the palpi and are still very usable although limited by awkward illustrations.

Plate 1. Unnamed *Dolichognatha* sp. from New Guinea hanging on debris; spider facing left.

Dolichognatha O. P.-Cambridge

Dolichognatha O. P.-Cambridge, 1869, Jour. Linnean Soc. London, 10: 387. Type species by monotypy *D. nietneri* O. P.-Cambridge, 1869, *ibid.*, p. 388, pl. 12, figs. 39–45, ♂, from Ceylon. Male holotype in the British Museum, Natural History, examined.

Landana Simon, 1883, Ann. Mus. Genova, 20: 184, erroneously placed in Archaeidae. Type species by monotypy *L. petiti* Simon, 1883, *ibid.*, p. 185, figs. 1–5, ♂, from the Congo. Male holotype in the Muséum National d'Histoire Naturelle, Paris, examined. NEW SYNONYMY.

Paraebius Thorell, 1894, Bihang Kongl. Svenska Vet.-Akad. Handl., 20: 43. Type species by monotypy *Paraebius mandibularis* Thorell, 1894, *ibid.*, p. 44. Male holotype from Sumatra in the Natural History Museum, Stockholm, examined. NEW SYNONYMY.

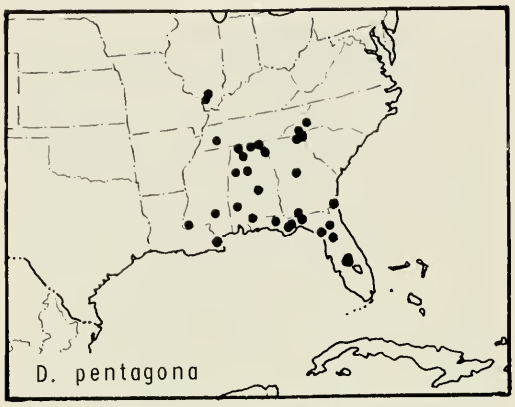
Prolochus Thorell, 1895, Descriptive catalog of the spiders of Burma, London, p. 122. Type species by monotypy *Prolochus longiceps* Thorell, 1895, *ibid.* Male holotype in the Natural History Museum, Stockholm, examined. NEW SYNONYMY.

Nicholasia Bryant and Archer, 1940, Psyche, 47: 60. Type species by monotypy *Epeira pentagona* Hentz, 1850. NEW SYNONYMY.

Afiamalu Marples, 1955, Jour. Linnean Soc. London, Zoology, 42: 495. Erroneously placed in Archaeidae. Type species by monotypy *Afiamalu richardi* Marples, 1955, *ibid.*, figs. 5, 7, 10, ♀, ♂, from western Samoa. NEW SYNONYMY.

Synonymies. Landana contains those species of *Dolichognatha* in which the males have longer chelicerae than females, and have the distal end of their chelicerae modified. As there are intermediates, it appears advisable to synonymize *Landana* with *Dolichognatha*. The *Paraebius* synonymy is uncertain. The male type examined lacked the characteristic four posterior abdominal humps. The cheliceral teeth were not all distal but spread out. The palpus is like that of *Dolichognatha*.

Prolochus belongs here, judging by the structure of the chelicerae, the palpus, and the poorly preserved abdomen. *Prolochus longiceps* differs in lacking pos-



Map 1. Distribution of *Dolichognatha pentagona* (Hentz).

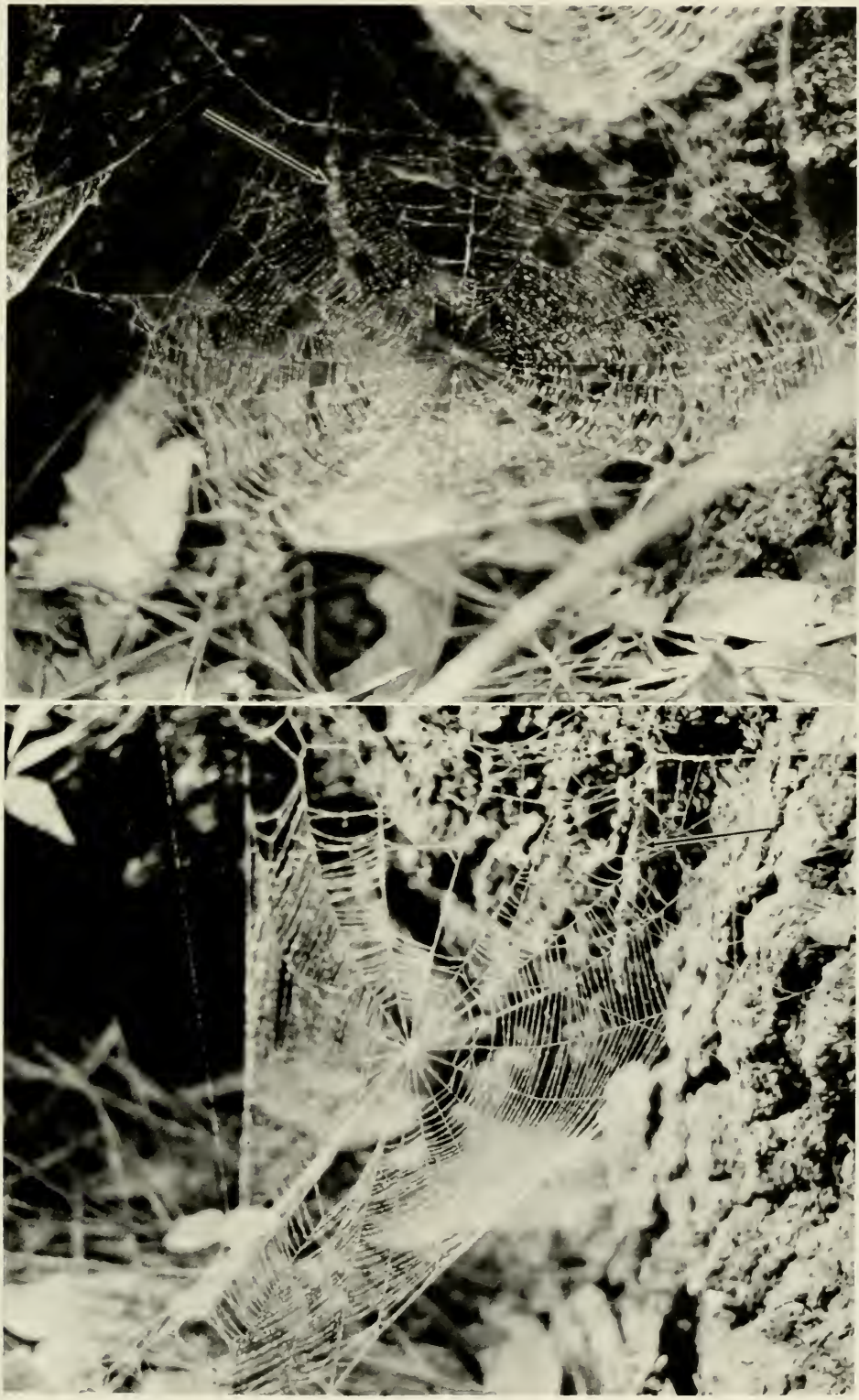
terior median eyes, but in some species of *Dolichognatha* the posterior median eyes are reduced in size. *Nicholasia* was erected by Bryant and Archer (1940: 60) for *D. heptagona*, which "differs from the Ceylonese genotype in the form of web, as well as in several important structural characters." Bryant and Archer repeated E. Simon's report (1894: 743) that *Dolichognatha* makes a horizontal sheet web. This is Simon's error. According to Bryant and Archer, *Nicholasia* differs from *Dolichognatha* by the "truncate tip of the labium, fewer teeth on the interior margin of the mandible and by the male palpus which has a dorsal apophysis on the basal third of the cymbium and a much simpler palpus." *Afiamalu* resembles *Landana* in "the shape of the carapace and in having spines on the legs, but differs in the armature of the chelicerae and the presence of a serrula [on the endites]."

Diagnosis. Dolichognatha, like other tetragnathids, lacks a tapetum in the secondary eyes, and the rhabdoms are arranged in looping rows (Figs. 7, 8). It differs from both *Tetragnatha* and *Azilia* in the shape of the abdomen: higher than long, with two pairs of posterodorsal humps (Plate 1; Figs. 1, 2, 10); it differs from *Tetragnatha* in lacking trichobothria on the femora. Like *Azilia*, but unlike *Tetragnatha* and *Pachygnatha, Dolichognatha* has a simple epigynum in the female (Fig. 6), and the male palpi do not have the cymbium modified (Fig. 13). Unlike *Azilia, Dolichognatha* exhibits a palpal paracymbium which is a complicated sclerite, different in different species (Fig. 13); it is not a free sclerite as in *Tetragnatha. Dolichognatha*'s most distinctive character is the shape and coloration of the carapace: head, often dark, with parallel sides, and carapace evenly rounded, always light-colored. The short-fanged chelicerae (Figs. 1–3, 10, 11) may be so long as to resemble those of Archaeidae, and if they are greatly elongated, the head may lose the characteristic parallel sides. The posterior median eyes touch (Figs. 2, 3, 11), or are only slightly separated. They may be minute in size or, among species previously placed in *Prolochus,* are lost completely.

Description. Carapace: head brown with darker marks; thorax yellow-white. Chelicerae usually brown. Sternum yellow-white with dark marks. Coxae yellow-white with dark spots. Legs contrastingly banded, dark bands narrow. Dorsum of abdomen with white and black pigments; abdominal humps are light-colored posteriorly, dark-colored anteriorly (Figs. 1, 2). Sides of abdomen dark posteriorly. Ventrally, area between genital groove and spinnerets with paired white patches and black pigment. Sides and head parallel if chelicerae small. Thoracic depression barely visible. Lateral eyes separated from each other by about their diameter (Figs. 1, 8, 10). Height of

→

Plate 2. Webs of *Dolichognatha pentagona*. Upper photograph, line of debris to the left of web's center (arrow), out of focus; web 12 cm diameter. Bottom photograph, with line of debris behind upper right outer spirals (arrow); web 7.5 cm diameter. Webs dusted with corn starch.



clypeus equal to diameter of the anterior median eyes. Anterior median eyes usually the largest (Figs. 3, 11). All lack tapetum, and secondary eyes have rhabdoms in rows as in *Tetragnatha* (Figs. 7, 8). Legs with strong macrosetae and sometimes denticles. Abdomen always higher than long and with four humps (Figs. 1, 2, 10). Femora without trichobothria, tibiae with a row or two, and metatarsi with one trichobothrium dorsally on the proximal end.

Epigynum lightly sclerotized and transverse (Fig. 6). Palpus simple, lightly sclerotized, except for the embolus (Figs. 13–15). Cymbium entire, with large attached paracymbium (P in Fig. 13).

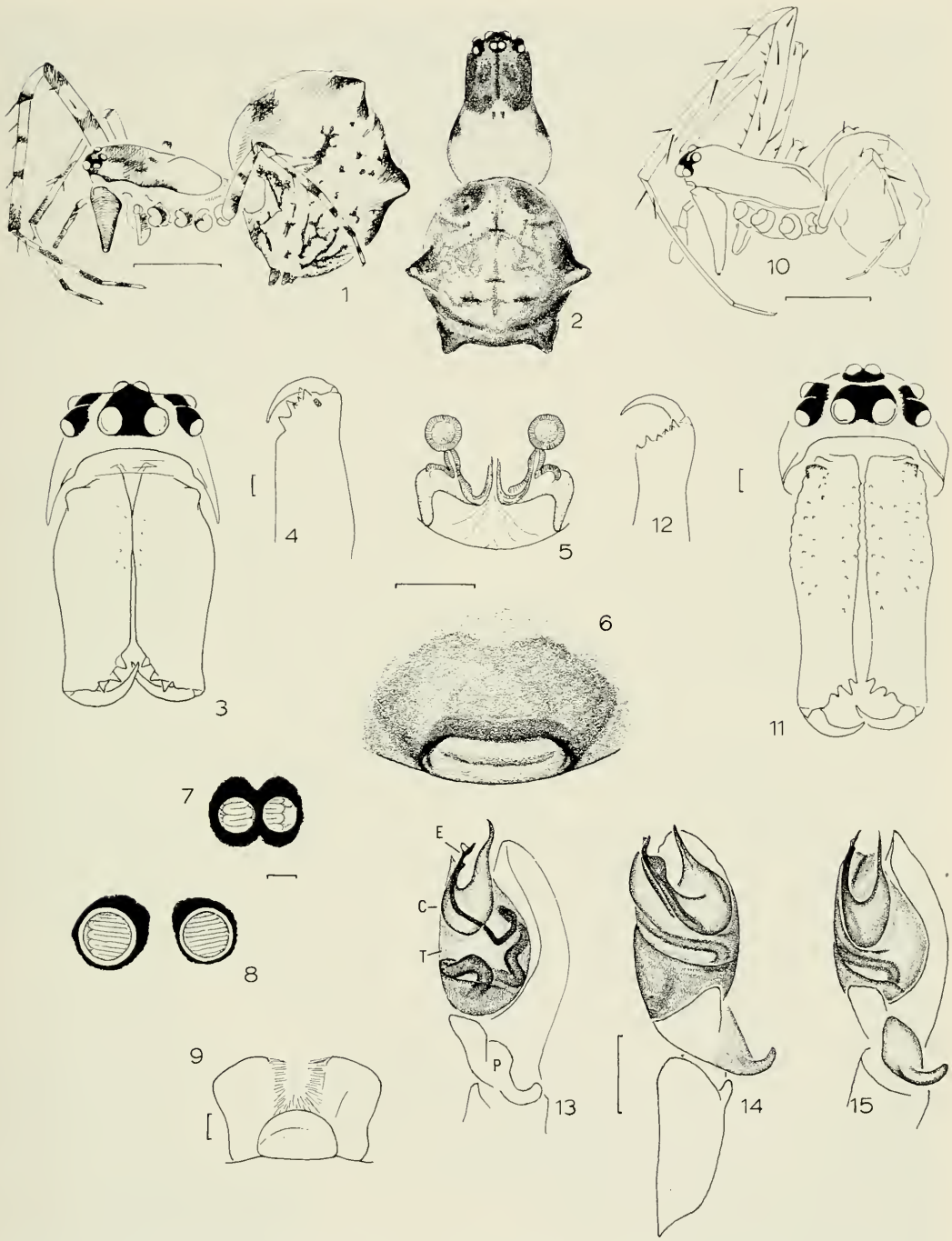
Natural History. I have seen the webs and habitats of four species of *Dolichognatha*: *D. pentagona* in the southeastern United States, two species in northern South America and one species in New Guinea. All constructed diagonal orb-webs between the buttress roots at the bases of large trees in relatively moist, dark forests. The web has a line of debris and egg-sacs across it or hanging vertically behind it (arrows, Plate 2). The spider rests among the debris. It is not surprising that collectors have at times marked specimens as an unknown species of *Cyclosa*. But the species is easily overlooked by collectors due to the specialized habitat, and individuals are not collected by sweeping. The web, often messy, does not stand out from other debris at the base of the tree, and the spider may not be on the web. Unlike other tetragnathids, *Dolichognatha* pulls the legs in at rest (Plate 1).

Species. Species of *Dolichognatha* are common worldwide in warm or tropical climates. The type species comes from Ceylon; there are specimens of different species from Africa in the Museum of Comparative Zoology collections. The genus is found in southeast Asia, and I have collected a species in New Guinea (Plate 1). Species differ only slightly in the shape of the abdomen and epigynum; there are greater differences in length and structure of chelicerae, in the internal female reproductive ducts, and in the structure of the paracymbium of the male palpus. Males of species with greatly elongated chelicerae also may have the cephalic carapace of diverse shapes and not have sides parallel as in *D. pentagona*. Males of some species have the fang groove at the distal end of the chelicerae modified and expanded. *Meta quadrituberculata* Keyserling, 1883, from Peru, belongs to the genus, as does *Cyclosa minuscula* Mello-Leitão.

Note. This genus does not belong to the family Archaeidae and is not related to *Archaea*, despite certain superficial resemblances. *Archaea*, unlike *Dolichognatha*, has scale-like body hair covering; has a more or less long, constricted neck between head and thorax; and has reduced lateral eyes. The endites of *Archaea* curve around the labium, and there is an elongate sternum. The unique spinnerets are the most important difference, and one that excludes the Archaeidae from the Araneoidea; the median spinnerets are minute, and the posterior spinnerets are much smaller than the anterior ones. *Zearchea* has only two spinnerets. The anal tubercle of *Archaea* is relatively large. The legs are thin and spindly, and there are only one or two trichobothria on the tibiae, one distally (unlike Araneoidea) on the metatarsus, none on the tarsus. The reduction of the spinnerets suggests association with the Zodarioidea; the loss of spinnerets is otherwise rare in Labidognatha.

Forster (1955) has illustrated an epigynum and a pair of seminal receptacles of archaeid spiders. His illustrations of archaeid palpi show few sclerites and much diversity among related species; the paracymbium is always absent. The sclerites are difficult to homologize with those of Araneoidea.

A key and illustrations to the Archaeidae of Madagascar can be found in Legendre (1970); a key to the genera was



Figures 1–15. *Dolichognatha pentagona* (Hentz). 1–9. Female. 1. Lateral. 2. Carapace and abdomen. 3. Eye region and chelicerae. 4. Left chelicera, posterior. 5. Epigynum, cleared, dorsal. 6. Epigynum. 7. Posterior median eyes. 8. Lateral eyes. 9. Labium and endites. 10–15. Male. 10. Left lateral. 11. Eye region and chelicerae. 12. Left chelicera, posterior. 13–15. Left palpus. 13. Lateral, expanded. 14. Ventral. 15. Lateral.

Scale lines. 0.1 mm; except Figs. 1, 2, 10, 1.0 mm.

Abbreviations. C, conductor; E, embolus; P, paracymbium; T, tegulum.

published by Forster (1955); and a list with distributions of all known species is in Legendre (1977).

Dolichognatha pentagona (Hentz), new combination

Plates 1, 2; Figures 1–15; Map 1

Epeira ? pentagona Hentz, 1850, J. Boston Soc. Natur. Hist., 6: 18, pl. 3, fig. 1, ♀. Specimens from Alabama, destroyed.

Cyrtophora tuberculata:—McCook, 1893, American Spiders, 3: 236, pl. 17, fig. 11, ♀. Probably not *D. tuberculata* Keyserling.

Dolichognatha tuberculata:—F. P.-Cambridge, 1903, Biologia Centrali-Americana, Araneidea, 2: 447. Probably not *D. tuberculata* Keyserling.

Nicholasia pentagona:—Bryant and Archer, 1940, Psyche, 47: 61, fig. 1, ♀, ♂. Archer, 1940, Paper Alabama Mus. Natur. Hist., 14: 27, pl. 2, fig. 1, web, pl. 5, figs. 1, 2, ♀, ♂.

Description. Female. Posterior median eyes 0.5 diameters of anterior medians; anterior laterals 0.8; posterior laterals 0.7 diameters of anterior medians. Posterior median eyes touching, 2.5 to 3 diameters from laterals (Figs. 1–3). The chelicerae are elongate with an anterior boss and a posterior hump (Figs. 1, 3, 10). There are three teeth on the anterior margin, two small ones on the posterior margins, and a longer one at the base of the fang (Fig. 4). Total length, 3.6 mm. Carapace, 1.7 mm long, 1.2 mm wide. First femur, 2.0 mm; patella and tibia, 2.4 mm; metatarsus, 1.6 mm; tarsus, 0.7 mm. Second patella and tibia, 1.9 mm; third, 1.0 mm; fourth, 1.2 mm.

Male, from Georgia. Eye arrangement as in female. Chelicerae much longer than those of female (Fig. 11). The palpus is rather small (Figs. 10, 14, 15). Total length, 3.2 mm. Carapace, 1.7 mm long, 1.1 mm wide. First femur, 2.2 mm; patella and tibia, 2.4 mm; metatarsus, 1.7 mm; tarsus, 0.7 mm. Second patella and tibia, 1.9 mm; third, 0.9 mm; fourth, 1.2 mm.

Variation. Total length of females, 2.6 to 4.0 mm; carapace, 1.6 to 1.8 mm long; first patella and tibia, 1.8 to 2.3 mm. Males vary from 2.6 to 3.2 mm in total length; carapace, 1.6 to 1.9 mm long; first patella and tibia, 2.2 to 2.7 mm.

Diagnosis. This species differs from others by the shape of the chelicerae (Figs. 3, 11), by the embolus and paracymbium in the small palpus (Figs. 14, 15), and by the shape of the ducts and seminal receptacles in the female (Fig. 5).

Natural History. This forest species makes its web between tree roots, just above the ground and at an angle nearly horizontal. Behind the web a vertical line of debris hangs from an upper frame thread, held together by silk and including egg-sacs (arrows, Plate 2). According to W. T. Sedgwick (personal communication), the spider rests at night in the hub of the web. During daytime the spider is among the line of debris. The species is probably much more common than records indicate; unless one especially searches for it, it is overlooked. The web is about 6 to 12 cm in diameter (Plate 2). Mature males and females can be found all summer.

Distribution. Southeastern states (Map 1). The northernmost record is from Little Grand Canyon, Jackson Co., Illinois, from several collections (J. Beatty).

Tetragnatha Latreille

Tetragnatha Latreille, 1804, Tableau méthodique des insectes, in Nouveau Dictionnaire d'Histoire Naturelle, 24: 135 (unavailable). Type species by monotypy is *T. extensa*. The name is feminine.

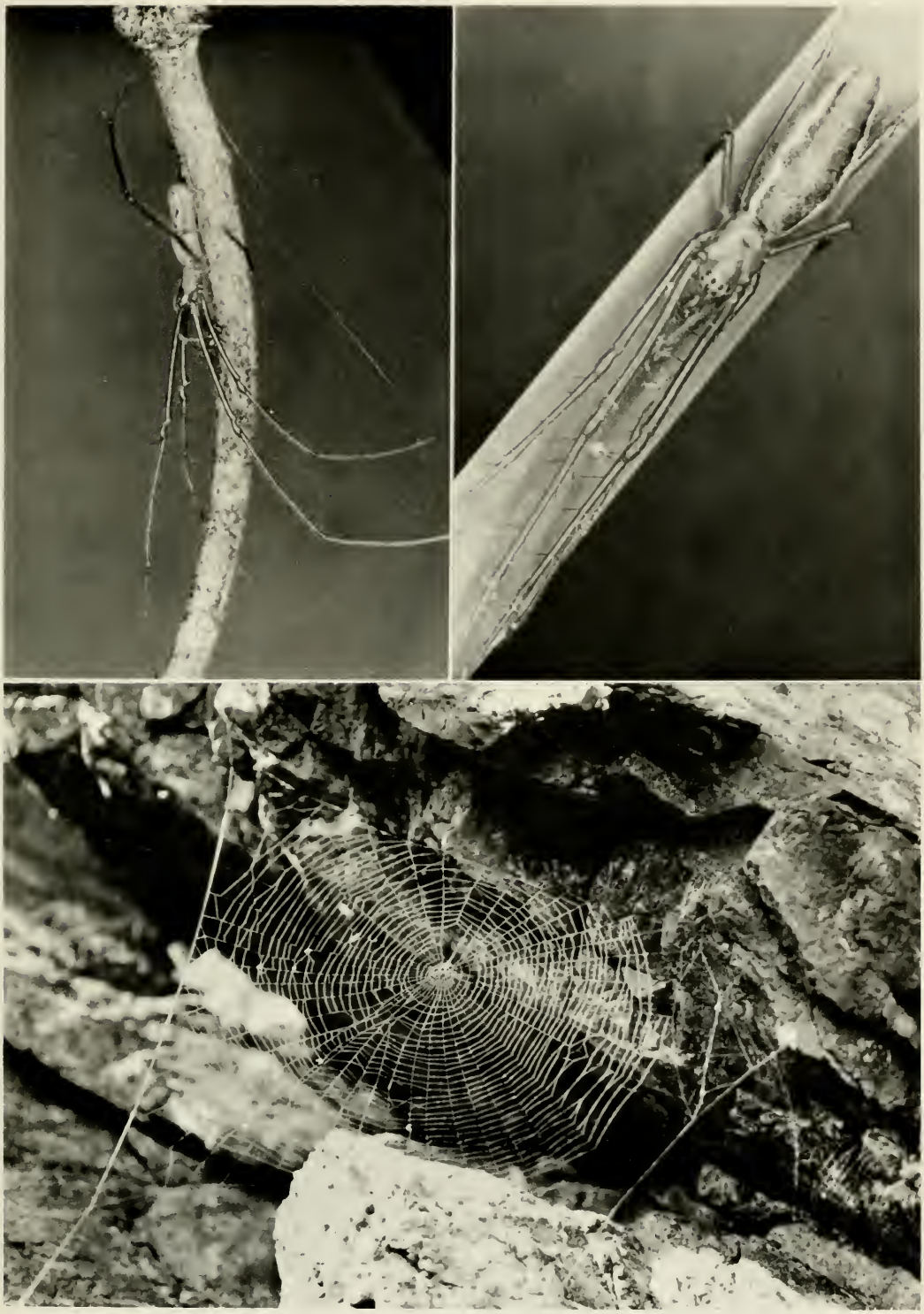
Eugnatha Audouin in Savigny, 1825, Explications sommaires des Planches d'Arachnides de l'Egypte et de la Syrie, p. 119. New name for *Tetragnatha* (an objective synonym).

Eucta Simon, 1881, Arachnides de France, 5: 5. Type species by monotypy is *E. gallica*.

Arundognatha Wiehle, 1963, Tetragnathidae in

→

Plate 3. Upper left, male *Tetragnatha versicolor*, Michigan; upper right, female *T. viridis*, Cape Cod; bottom, web of *T. versicolor* with closed hub, Friday Harbor, Washington (web photo B. Opell).



Tierwelt Deutschlands, 49: 47. Type species *T. striata* L. Koch designated by Wiehle.

Note. The characters that separate *Eucta* and *Arundognatha* from *Tetragnatha* are not those of distinct groups. The two North American species with tails (=*Eucta*), *T. caudata* (Figs. 140–148) and *T. branda* (Figs. 167–175), are not closely related. Judging by similarity of genitalia, *T. caudata* is close to *T. pallescens*; both have the conductor tipped by a hook (Figs. 139, 148). *Tetragnatha branda* is close to *T. vermiformis*; both lack the pleat next to the conductor (Figs. 175, 184); females of both have the seminal receptacles on each side dorsoventral to each other (Figs. 170, 179).

Some rare specimens of *T. laboriosa* have the lateral eyes farther apart than medians, and could be included in *Arundognatha*. But, most have the lateral eyes slightly closer together than the medians. *Tetragnatha laboriosa*, judging by the genitalia, is close to *T. versicolor*, *T. viridis*, and *T. pallescens*. *Tetragnatha versicolor* always has the lateral eyes closer than the medians; *T. viridis*, the same distance apart; *T. pallescens*, always farther apart. All belong to the same species group.

Diagnosis. Tetragnatha differs from *Pachygnatha* and *Glenognatha* by lacking a tapetum in the lateral eyes (Figs. 21, 22); it differs from *Dolichognatha* as well as from the two previous genera by having an elongate to tubular-shaped abdomen (Fig. 23), usually with silver pigment. It further differs from *Dolichognatha* in lacking an epigynum and by having trichobothria on the femora (Fig. 17). It differs from *Leucauge* by lacking tapetum in the secondary eyes.

Description. Carapace slightly elongate, weakly sclerotized, lacking setae, and often with an indistinct median longitudinal gray band. Eyes on black spots. Sternum weakly sclerotized, surrounding coxae (Fig. 16). Chelicerae and legs yellowish white to brown. Abdomen silver, consisting of tiny pigment spots least dense on venter, most dense on dorsum. Dorsum either has gray or black folium, or lacks pigment and folium altogether; the venter may have a median longitudinal dark band.

Eyes closely grouped, lateral eyes less than two diameters from medians (Figs. 24, 31). The lateral eyes may touch, but more commonly are slightly separated or far apart, with the anterior lateral eyes having moved away in an anterior lateral direction (Figs. 177, 182). The placement of the eyes is somewhat variable within species. Clypeus height equals one to two diameters of anterior median eyes (Figs. 24, 130). Chelicerae more or less enlarged, often with complex teeth (Figs. 24, 25, 31). Labium rebordered (distally swollen); endites elongate and distally widened (Fig. 16). Legs very long, first longest, third shortest. Abdomen cylindrical, often swollen anteriorly (Fig. 23) or with sides almost parallel (Fig. 149); in some species a tail overhangs spinnerets (Figs. 140, 167).

Males are only slightly smaller than females. Male chelicerae are larger and more projecting than those of female, with a spur (apophysis) on anterior face to hold the female fang when mating (Figs. 31, 52). The chelicerae have a very long tooth (the main tooth) distally from a row of smaller teeth (Figs. 62, 80) (absent in *T. dearmata* and *T. pallescens*). These smaller teeth become progressively smaller proximally. Distal from the large tooth is a slanting tooth (Figs. 62, 80), and at the base of the fang a smaller knob called a fang guide (Locket and Millidge, 1953; Wiehle, 1963). The dentition is much more complex in many species (Figs. 24, 31).

→

Plate 4. Above, female *Tetragnatha pallescens*, Florida; below, mating *T. straminea*, Massachusetts, male on left with left palpus inserted, right palpus held forward (photo J. Coddington).

There are trichobothria on each femur (Fig. 17). *Tetragnatha laboriosa* females have 13 trichobothria on the first femur, 11 on the second, 11 on the third, and 13 on the fourth. There are the usual trichobothria on the tibiae, and there is one trichobothrium on the third metatarsus.

Genitalia. The male palpus is slightly more complex than that of *Pachygnatha.* A spherical tegulum (T in Figs. 19, 20) encloses the duct. The duct makes only a single coil. The filiform embolus (E) is distally wrapped within a complex conductor (Figs. 19, 20). The cymbium (Y) appears more complex than that of other araneids; it is small and may be more or less lobed (Figs. 18–20). The paracymbium (P) is a separate sclerite (Fig. 18) as in *Pachygnatha* and the family Linyphiidae.

The paracymbium (P) is straight, but usually has a small lobe on the lateral cymbium side (Fig. 18). *Tetragnatha guatemalensis* and *T. earmra* have a distal finger projecting from the paracymbium (Figs. 44, 54); that of *T. nitens* has a large ventral transparent lobe and a distal notch (Fig. 33). In other species the paracymbium is not diagnostic.

The most complex part of the palpus is the conductor (C in Figs. 19, 20 and Plates 5–7), which often has pleats laterally (L in Fig. 45). These pleats are absent in *T. branda* (Fig. 175), *T. vermiformis* (Fig. 184), the European *T. striata,* and the cosmotropical *T. nitens* (Fig. 34). When expanded, it can be seen that the pleats enlarge, since they are hematodocha (C in Figs. 19, 20). The distal tip of the conductor is sclerotized and seems the most useful character for identifying species (Plates 5–7).

The female genitalia are quite similar to those of *Pachygnatha* (Levi, 1980a). There is no epigynum; the genital openings are at the posterior end of a median ventral lobe from the epigastric area (Fig. 26). The seminal receptacles are anterior, near the level of the lung spiracles; there are two on each side (Fig. 48), only one in *T. nitens* (Fig. 27). There is a median, lightly sclerotized structure, comprising the so-called median seminal receptacles (Figs. 27, 48), which probably hold the conductor when mating. The shape and position of the seminal receptacles are the most useful species diagnostic characters of females.

Species. There are *Tetragnatha* species on all continents and islands, and in arctic, temperate, and tropical climates.

Judging by the similarity of the genitalia, most of the North American species are closely related to each other: *elongata, versicolor, viridis, laboriosa, pallescens, caudata, straminea,* and probably *shoshone.* The cosmotropical *T. nitens* is distinct from any other species in the area: it has only two seminal receptacles (Fig. 27) and, like *T. vermiformis,* lacks the pleats on the palpal conductor (Fig. 34). *Tetragnatha vermiformis* (Figs. 176–184) and *T. branda* (Figs. 167–175) I believe are closely related to the European *T. striata. Tetragnatha guatemalensis* and *T. earmra* belong to a fourth group, judging by the more specialized paracymbium (Figs. 44, 54) and tip of the conductor (Figs. 45, 55). *Tetragnatha extensa* and *T. dearmata* are closest to the first group mentioned and perhaps to Old World relatives of the *T. versicolor* group.

Species that have the lateral eyes relatively close together also have the largest amount of black pigment, and have the abdomen swollen anteriorly. Species that have the lateral eyes far apart tend to have less dark pigment; the abdomen tends to be tubular and silvery.

Diagnostic Species Characters. The best characters to separate species are: in males, the shape of the conductor tip (Plates 5–7); in females, the shape and position of the seminal receptacles, which can be seen only after lifting the exoskeleton of the genital lobe on one side (see Methods of Study). Coloration, amount of black pigment, and the distance between the lateral eyes are help-

ful. The chelicerae, faithfully illustrated by earlier authors, have unique characters in only a few species.

However, the separation of *Tetragnatha* species is still reasonably difficult. While the distance between lateral eyes compared with the distance between medians is an excellent superficial character, there is considerable variation within species, perhaps most noticeable in *T. laboriosa*. Most *T. laboriosa* have the lateral eyes slightly closer together than the medians, but some have them the same distance apart, and in some specimens they are slightly farther apart.

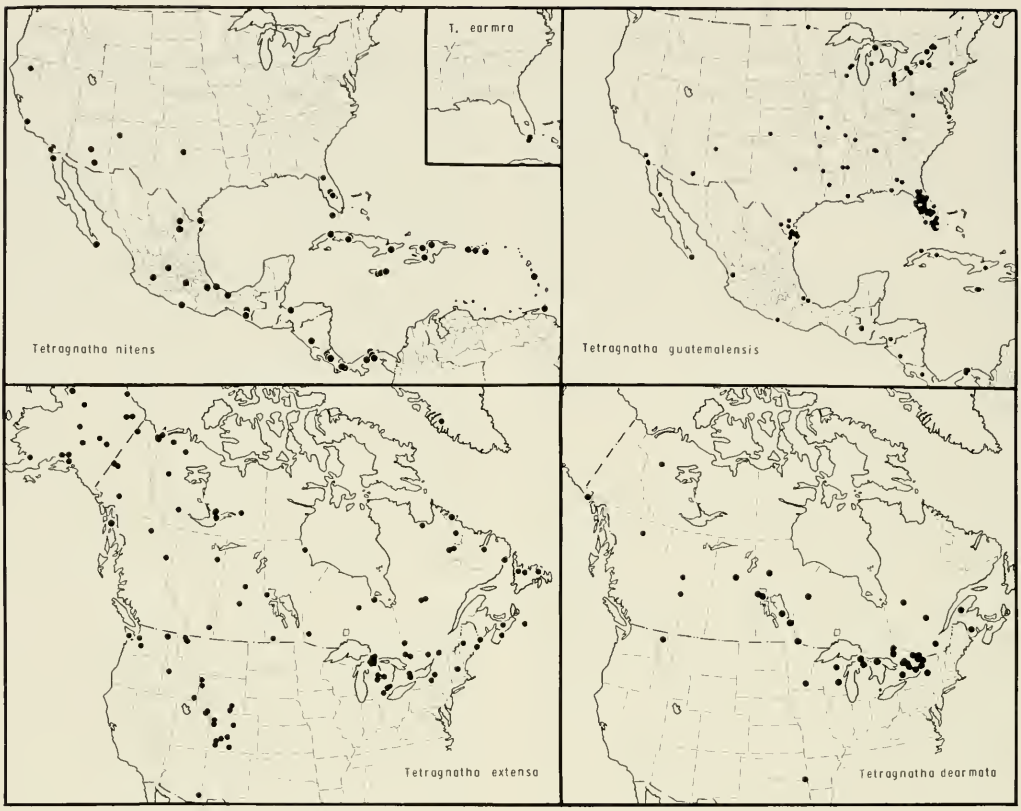
Many of the old North American published records of *Tetragnatha* species were based on determinations of juvenile specimens or adults, using chelicerae, and are in error.

Natural History. Most *Tetragnatha* species are found near water. Some may seem rare only because spider collectors are generally terrestrial (e.g., *T. branda* and *T. vermiformis*). The most abundant species in collections, *T. laboriosa* and *T. versicolor,* are the two species living farthest away from water. Several species have very specialized habitats: *T. viridis* is found in conifers, especially pines; the European *T. pinicola* is also found in trees. The rarity of *T. viridis* may reflect its reluctance to drop within reach. *Tetragnatha branda* has been collected only from salt marshes.

The orb-web ranges from horizontal to vertical. The hub, usually but not always open (Plate 3), is cut out after the web is completed (Wiehle, 1963). The spider rests on a plant or in the middle of the web, legs extended in a paraxial direction (Plates 3, 4). The web of *T. laboriosa* is made in the evening, before nightfall (Le Sar and Unzicker, 1978), as is the web of *T. nigrita* (Wiehle, 1963), and perhaps of other species as well. According to Crome (1954), *Tetragnatha kaestneri* (= *Eucta kaestneri*) does not make a scaffolding before the viscid spiral.

Tetragnatha laboriosa makes its web only when temperatures are warm and it is not windy. It seeks a new location each night; the web size is controlled by the physical dimensions of the space between vegetation. The spiders feed most actively from sundown until just after dark (Le Sar and Unzicker, 1978). *Tetragnatha* feed nonselectively on dipterans, but Le Sar reports that their *T. laboriosa* also feeds on Miridae and Cicadellidae. The importance of *Tetragnatha* as a mosquito predator has been described in papers by Łuczak and her colleagues (1966, 1968, 1970). Adults of North American species are found almost all summer, and live for the season; perhaps there are two generations in summer (Le Sar and Unzicker, 1979). The males are almost as common as females, and therefore must have a similar life span.

There is no obvious courtship. The male grasps the female's chelicerae with his fangs (Plate 4); the coupling is apparently so secure that no holdfast organ is necessary adjoining the copulatory opening (epigynum). Perhaps this is the circumstance that has permitted the loss of the epigynum. The female may coil her abdomen while mating. Palpi are alternated, as in most entelegyne spiders (Plate 4). Unlike most other Araneidae, the male does not court between the use of left and right palpi. Like haplogyne spiders and Palpimanidae, males may use both palpi together in sperm induction. A week after mating, the female may produce several egg-sacs, fluffy structures broadly attached to vegetation. The young hatch soon thereafter and overwinter in immature stages. Adults of the specialized *T. viridis* are only found in late spring. In one instance a late August young was raised. It readily fed on the drosophila flies which were caught without web (in a vial) and matured in December in the laboratory after two molts. As an adult male, it continued to feed on drosophila flies. Łuczak and Dąbrowska-Prot (1966) also describe the ability of



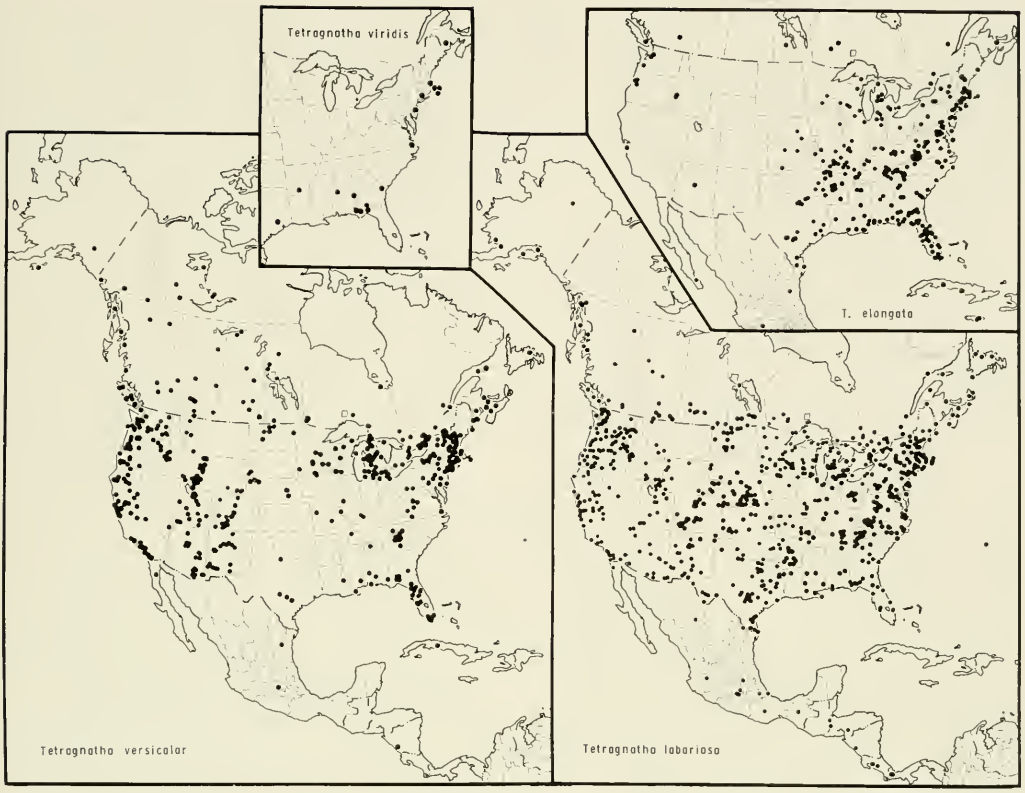
Map 2. Distributions of *Tetragnatha nitens* (Audouin), *T. earmra* n. sp., *T. guatemalensis* O. P.-Cambridge, *T. extensa* (Linnaeus), and *T. dearmata* Thorell in North America.

Tetragnatha to catch flies without the use of webs.

Key to Species. The distance of the lateral eyes from each other compared to the distance of the median eyes is an easy character to see. The distance is measured from the center of the eyes. Unfortunately there is considerable variation, especially in the commonest species, *T. laboriosa*. While in most specimens of this species the lateral eyes are slightly closer together than the medians or an equal distance apart, in a very rare specimen the eyes are very slightly farther apart.

KEY TO FEMALE *TETRAGNATHA* NORTH OF MEXICO

1. Lateral eyes farther apart than medians (Figs. 130, 141, 150, 159, 168, 177) 2
– Lateral eyes as far apart as medians or closer together (Figs. 24, 36, 75, 111) 7
2(1). Abdomen with a tail extending beyond spinnerets (Figs. 140, 167) 3
– Abdomen without a tail (Figs. 129, 176) 4
3(2). Anterior median seminal receptacles closer to each other than to other member of pair (Figs. 142, 143); Canada, Northwest, eastern states (Map 4) ..... *caudata*
– Anterior and posterior seminal receptacles on each side next to each other (Figs. 169, 171); New England to Gulf Coast (Map 4) ..... *branda*
4(2). Abdomen only silver on dorsal half, edge of silvery area forming a lateral line with area below lacking silver pigment (Fig. 149); seminal receptacles on each side about 1 to 2 times their diameter apart and connected by a stalk (Fig. 153); Alberta, Utah, and East (Map 4) ..... *straminea*



Map 3. Distributions of *Tetragnatha elongata* Walckenaer, *T. versicolor* Walckenaer, *T. viridis* Walckenaer, and *T. laboriosa* Hentz.

– Abdomen all silvery, except for midventer (Fig. 158); seminal receptacles otherwise (Fig. 162) 5

5(4). Seminal receptacles elongate, paraxial, and members of a pair on top of one another (Figs. 178, 180); abdomen at most 3 times longer than wide or high (Fig. 176); Ontario, northwest to Florida (Map 4) ..... *vermiformis*

– Seminal receptacles pear-shaped and side by side (Figs. 131, 133, 160, 162); length of abdomen about 4 or 5 times width or height (Figs. 129, 158) 6

6(5). Members of pair of seminal receptacles on each side almost touching (Fig. 162); Great Slave Lake, Ontario, Indiana to Pacific (Map 4) ..... *shoshone*

– Members of pair of seminal receptacles on each side separated by an intermediate lobe (Fig. 133); widespread (Map 4) ..... *pallescens*

7(1). Genital cover twice as long as wide, narrowed anteriorly, posterior rim notched (Fig. 26); only two seminal receptacles (Fig. 27); Florida, Texas, California (Map 2) ..... *nitens*

– Genital cover square or wider than long (Figs. 49, 77); four seminal receptacles (Figs. 50, 69, 78) 8

8(7). Lateral eyes about as far apart as medians or slightly closer together (Figs. 57, 111, 121) 9

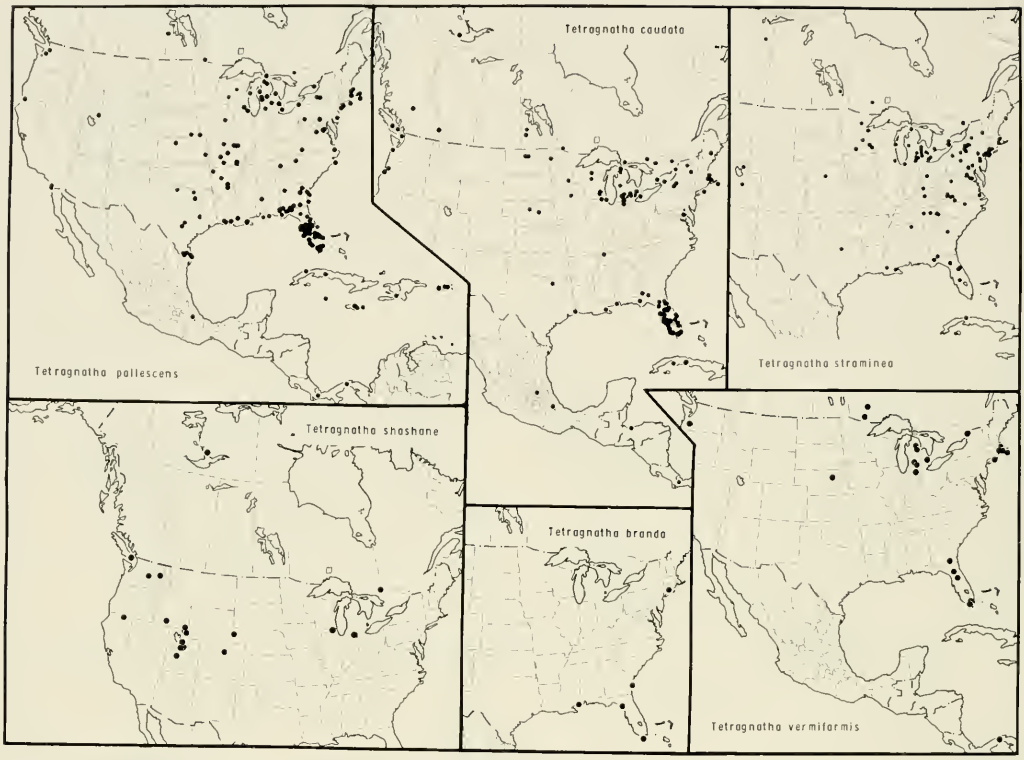
– Lateral eyes clearly closer together than medians (Figs. 47, 66, 75, 91) .. 11

9(8). Green; first and second tibial macrosetae length 3 to 5 times diameter of article (Fig. 115); New Brunswick to eastern Texas (Map 3) ..... *viridis*

– Silvery and yellowish white; macrosetae length at most 3 times diameter of article 10

10(9). Prominent pouch between pair of seminal receptacles hiding anterior one in ventral view; posterior seminal receptacle pear-shaped (Fig. 124); widespread (Map 3) ..... *laboriosa*

– No pouch between members of pair of seminal receptacles; posterior seminal



Map 4. Distributions of *Tetragnatha pallescens* F. P.-Cambridge, *T. caudata* Emerton, *T. straminea* Emerton, *T. shoshone* n. sp., *T. branda* n. sp., and *T. vermiformis* Emerton.

receptacle elongate and transverse (Fig. 60); Alaska, Canada, northeastern states, Rocky Mountains (Map 2) ... *extensa*

11(8). Anterior seminal receptacles of each pair elongate, paraxial, parallel to receptacle of other pair (Figs. 76, 78); widespread (Map 2) ..... *elongata*

– Anterior seminal receptacles oval or pear-shaped; if elongate, not placed parallel (Figs. 39, 69) 12

12(11). Seminal receptacles of each pair on top of one another, paraxial (Figs. 39, 50) 13

– Seminal receptacles of each pair side by side (Figs. 69, 94) 14

13(12). Seminal receptacles elongate-oval (Fig. 50); widespread (Map 2) ..... *guatemalensis*

– Seminal receptacles subspherical (Fig. 39); Everglades and Florida Keys (Map 2) ..... *earmra*

14(12). Posterior lateral seminal receptacle of each pair U-shaped (Fig. 69); Alaska to northern States (Map 2) ..... *dearmata*

– Posterior lateral seminal receptacle of each pair oval (Fig. 94); widespread (Map 3) ..... *versicolor*

Key to Male *Tetragnatha* North of Mexico

1. Lateral eyes farther apart than medians (Figs. 137, 146, 155, 164, 173, 182) 2

– Lateral eyes as far apart as medians or closer together (Figs. 31, 52, 71, 80, 126) 7

2(1). Abdomen with a tail extending beyond spinnerets (Figs. 145, 172) 3

– Abdomen without tail (Figs. 136, 181) 4

3(2). Conductor with lateral pleats (Figs. 147, 148); tip bird head-shaped with a lateral spur (Fig. 148; Plate 7c); Canada, northwest to eastern states (Map 4) ..... *caudata*

– Conductor without lateral pleats (Figs. 174, 175), tip with lateral notch (Fig. 175; Plate 7g, h); New England to Gulf Coast (Map 4) ..... *branda*

4(2). Conductor without pleats (Figs. 183, 184); tip tapering to a point, small, bent over (Fig. 184; Plate 7i); Ontario, northwest to Florida (Map 4) ..... *vermiformis*

– Conductor with pleats (Figs. 138, 139); tip large with a neck (Figs. 138, 166) 5

5(4). Tip of conductor a large recurved hook (Fig. 139; Plate 7a); widespread (Map 4) ..... *pallescens*

– Tip of conductor not a large recurved hook (Figs. 157, 166) 6

6(5). Tip of conductor with a narrow neck (Figs. 156, 157; Plate 7d); only dorsal half of abdomen silver (Fig. 154); Alberta, Utah, and East (Map 4) ..... *straminea*

– Tip of conductor with a wide neck (Figs. 165, 166; Plate 7e, f); abdomen except for midventer all silver (Fig. 163); Great Slave Lake, Ontario, Indiana to Pacific (Map 4) ..... *shoshone*

7(1). Paracymbium with distal notch or with distal finger (Figs. 33, 44, 54) 8

– Paracymbium not modified, distally rounded (Figs. 18, 20, 81) 10

8(7). Paracymbium wide with distal notch (Fig. 33); conductor without pleats (Fig. 34; Plate 5a, b); Florida, Texas to California (Map 2) ..... *nitens*

– Paracymbium narrow with distal finger (Figs. 44, 54) 9

9(8). Chelicerae about half length or longer than carapace (Figs. 51, 52); conductor tip with lateral finger (Fig. 55; Plate 5d); widespread (Map 2) ..... *guatemalensis*

– Chelicerae about half carapace length (Figs. 40–42); tip of conductor crescent-shaped in ventral view, concave laterally (Fig. 45; Plate 5c); Everglades and Keys (Map 2) ..... *earmra*

10(7). Conductor tip with neck and sclerotized on lateral side, pointing laterally to side of paracymbium (Figs. 63, 64; Plate 5e); Alaska, Canada, northeastern states, Rocky Mountains (Map 2) ..... *extensa*

– Conductor tip pointed distally, recurved or pointing mesally (Figs. 73, 82, 128; Plates 5f, g, 6b, h) 11

11(10). Conductor tip bird head-shaped (Fig. 128; Plate 6h, i); pleat closest to conductor lifted up (Fig. 128); widespread (Map 3) ..... *laboriosa*

– Conductor tip otherwise (Figs. 73, 82, 98, 119); pleats' curvature about parallel to conductor (Figs. 73, 82) 12

12(11). Lateral eyes about as far apart as medians (Fig. 117); green; length of first and second tibial macrosetae 3 to 5 times diameter of article (Fig. 115); New Brunswick to eastern Texas (Map 2) ..... *viridis*

– Lateral eyes closer together than medians (Figs. 80, 96); silver-brown to gray; length of first and second tibial macrosetae at most 3 times diameter of article 13

13(11). Conductor tip tapering to a minute point, conductor concave laterally near tip (Fig. 82; Plate 5g, h); chelicerae usually longer than carapace (Figs. 79, 80); widespread (Map 3) ..... *elongata*

– Conductor tip otherwise (Figs. 73, 98); chelicerae usually shorter than carapace (Figs. 70, 71, 95, 96) 14

14(13). Conductor tip a pennant, pointing mesally (Figs. 72, 73; Plate 5f); Alaska to northern states (Map 2) ..... *dearmata*

– Conductor tip a recurved hook (Fig. 98, 105–109; Plate 6b–f); widespread (Map 2) ..... *versicolor*

Tetragnatha nitens (Audouin in Savigny) Plate 5a, b; Figures 23–34; Map 2

Eugnatha nitens Audouin in Savigny, 1825, Explication sommaire des Planches d'Arachnides de l'Egypte et de la Syrie, p. 118, pl. 2, fig. 2, ♀. Specimens from near Rosetta [Rashid], Egypt, lost.

Eugnatha pelusia Audouin in Savigny, 1825, Explication sommaire des Planches d'Arachnides de l'Egypte et de la Syrie, p. 119, pl. 2, fig. 3, ♂. Specimen from island of Rosetta [Rashid], Egypt, lost. NEW SYNONYMY.

Tetragnatha andina Taczanowski, 1878, Horae Soc. Entom. Rossicae, 14: 144, pl. 1, fig. 2, ♀. Numerous female and male syntypes from Amable María, Prov. Tarma, Peru in the Polish Academy of Sciences, examined. NEW SYNONYMY.

Tetragnatha antillana Simon, 1897, Proc. Zool. Soc. London, p. 868. 13 male and 17 female and 5 juvenile syntypes from St. Vincent Island, Lesser Antilles, in the British Museum, Natural History, examined. Seeley, 1928, Bull. New York State Mus, 278: 105, figs. 1–4, ♀, ♂. Roewer, 1942, Katalog der Araneae, 1: 988. Chickering, 1957, Bull. Mus. Comp. Zool., 116:306, figs. 1–6, ♀, ♂; Breviora, 68: 2. Bonnet, 1959, Bibliographia Araneorum, 2: 4318. Chickering, 1962, Bull. Mus. Comp. Zool., 127: 428, figs. 1–6, ♀, ♂. NEW SYNONYMY.

Tetragnatha vicina Simon, 1897, Proc. Zool. Soc. London, p. 869. Three male syntypes from St. Vincent, Lesser Antilles in the British Museum, Natural History, examined. NEW SYNONYMY.

Tetragnatha peninsulana Banks, 1898, Proc. California Acad. Sci., ser. 3, 1: 246, pl. 15, fig. 12, ♀, ♂. Four female syntypes from San José del Cabo, Baja California in the Museum of Comparative Zoology, examined. Male syntype in California Academy of Sciences, destroyed. NEW SYNONYMY.

Tetragnatha galapagoensis Banks, 1902, Proc. Washington Acad. Sci., 4: 61, pl. 1, fig. 10, ♀, ♂. One male, one female syntype from Galápagos

Islands in the Museum of Comparative Zoology, examined. NEW SYNONYMY.

Tetragnatha aptans Chamberlin, 1920, Bull. Brooklyn Mus. Sci., 3: 41, figs. 7, 8, ♀. Female paratypes from Chincha Island, Peru in the Museum of Comparative Zoology, examined.

Tetragnatha eremita Chamberlin, 1924, Proc. California Acad. Sci., ser. 4, 12: 645, figs. 89, 90, ♂. Right male palpus of holotype from Puerto Escondido, Baja California in the Museum of Comparative Zoology, examined. NEW SYNONYMY.

Tetragnatha seminola Gertsch, 1936, Amer. Mus. Novitates, no. 852: 10, figs. 22, 23, ♂. Male Holotype from the northeast shore of Lake Okeechobee, Florida in the American Museum of Natural History, examined. NEW SYNONYMY.

Tetragnatha steckleri Gertsch and Ivie, 1936 Amer. Mus. Novitates, no. 858; 19, figs. 31–3?, ♀, ♂. Male holotype from Tucson, Arizona in the American Museum of Natural History, examined. NEW SYNONYMY.

Tetragnatha nitens:—Roewer, 1942, Katalog der Araneae, 2: 978. Bonnet, 1959, Bibliographia Araneorum, 2: 4345. Okuma, 1968, Acta Arachnologica, 21: 40, figs. 9–16, ♀, ♂.

Tetragnatha elmora Chamberlin and Ivie, 1942, Bull. Univ. Utah, biol. ser., 7(1): 62, fig. 160, ♀. Female holotype from Bluewater Lake, New Mexico in the American Museum of Natural History, examined. NEW SYNONYMY.

Tetragnatha festina Bryant, 1945, Bull. Mus. Comp. Zool., 95: 407, figs. 38, 39, 41, ♂ (not ♀). Male holotype from foothills of Cordillera Central, south of Santiago, Dominican Republic in the Museum of Comparative Zoology, examined. NEW SYNONYMY.

Tetragnatha haitensis Bryant, 1945, Bull. Mus. Comp. Zool., 95: 408, fig. 37, ♀. Female holotype from Ennery, Haiti in the Museum of Comparative Zoology, examined.

Note. Roewer (1942) cites the page of Savigny as 323 and the date as 1827. This is a later printing of the work. Plate 2c of Audouin in Savigny shows the diagnostic posterior cusp on the fang of the female. The posterior distal cheliceral teeth of the female are shorter in Audouin's illustration than those in our specimens. *Tetragnatha pelusia* has never before been synonymized with *T. nitens*, although the palpus and chelicerae are illustrated and the illustrations are more diagnostic than those of the female.

Variation. The length of the palpal tibia may be greater or less than the cymbium. The lateral eyes are sometimes as far apart as the medians, usually slightly closer together. On Panamanian specimens the diagnostic tooth at the posterior base of the fang is as long as the chelicerae are wide, and is sometimes smaller than illustrated on the most northern specimens. Total length of females, 7.4 to 11.0 mm; total length of males, 5.2 to 10.1 mm.

Diagnosis. Both sexes of this species are easily separated from other North American species. The lateral eyes are as far apart as the medians, sometimes closer together or, rarely, farther apart. There are gray pigment marks on the body (Fig. 23).

The paracymbium of the male palpus has a distal notch and a ventral transparent lobe (Fig. 33); the conductor lacks pleats along the distal edge (Plate 5a; Fig. 34).

The female chelicerae have a large posterior lateral tooth at the insertion of the fang (Figs. 24, 25) and a cusp posteriorly on the base of the fang (sometimes absent) (Fig. 25); the genital area is longer than wide, constricted anteriorly, with a notch above the opening (Fig. 26). Unlike all other North American species, there are only two seminal receptacles (Fig. 27). The female chelicerae are as long as the carapace or longer (Figs. 23, 24).

Natural History. The species has been collected above wet ground and near a creek in Mexico, and in woods in Puerto Rico.

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Plate 5. *Tetragnatha* male, left palpi; scanning electron micrographs of conductors and their tips. a, b, *T. nitens*, compare to Fig. 34. c, *T. earmra* (tip broken on right), compare with Fig. 45. d, *T. guatemalensis*, compare to Fig. 55. e, *T. extensa*, compare to Fig. 64. f, *T. dearmata*, compare to Fig. 73. g, i, *T. elongata*, compare to Fig. 82. (g, h, locality unknown; i, Florida). *Scale lines.* 0.05 mm.

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Distribution. Cosmotropical, in North America north to northern Florida, northern Texas, New Mexico to northern California (Map 2). Since there are several similar species in tropical America, including *T. peruviana* Taczanowski and *T. piscatoria* Simon, *T. nitens* may have originated in South America.

Records. Florida. Alachua Co.: Gainesville; Newnan's Lake. Glades Co.: NE shore of Lake Okeechobee. Highlands Co.: Sebring. Monroe Co.: Johnston Key. *Texas.* Baylor Co.: Mabelle. Hidalgo Co.: Hargill. *New Mexico.* Valencia Co.: Bluewater Lake. *Arizona.* Maricopa Co.: Salt River near Blue Point. Pima Co.: Tucson. *California.* San Diego Co.: Escondido Reservoir; San Diego Mission. San Louis Obispo Co.: Atascadero Lake. Shasta Co.: McArthur.

The Museum of Comparative Zoology has specimens from several areas not shown on Map 2. *Galápagos Islands. Peru.* Chincha Isl. *Brazil.* Rio dos Macacos; Mendez; São Paulo. *Paraguay.* Río Paraná; 75 km NE Concepción; Hernandrías. *Madagascar. New Zealand.*

Tetragnatha earmra new species
Plate 5c; Figures 35–45; Map 2

Holotype. Male from Earmra South East Island, Everglades National Park, Florida, 28 January 1973 (A. Sheldon), in the Museum of Comparative Zoology. The name is an arbitrary combination of letters.[2]

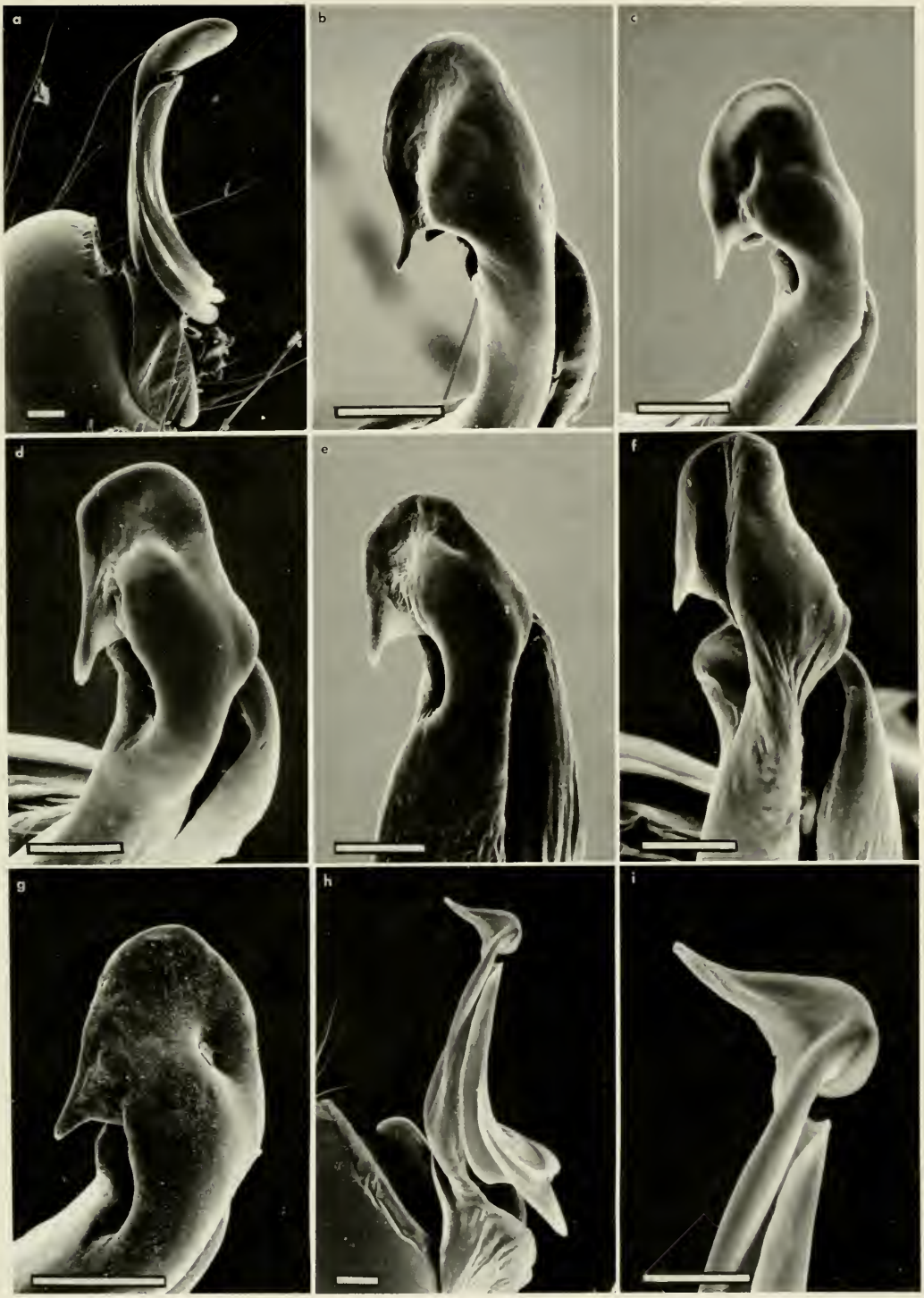
Description. Female. Carapace brown, head region darker. Chelicerae brown; labium dark, except for swollen area. Sternum dark brown, legs brown. Eyes with distinct black rings (Fig. 36). Dorsum and abdomen with several pairs of dark patches on sides (Fig. 35). Venter with black band having parallel sides (Fig. 35). The lateral eyes are closer to each other than the medians, and situated together on a tubercle (Fig. 36). Posterior eyes 0.8 diameters of anterior medians; anterior laterals 0.5 diameters of anterior medians. Anterior median eyes their diameter apart, slightly less than two diameters from laterals. Posterior median eyes about 4 diameters apart, slightly less than four diameters from laterals. Total length, 6.0 mm. Carapace, 1.9 mm long, 1.3 mm wide. First femur, 4.2 mm; patella and tibia, 5.1 mm; metatarsus, 4.3 mm; tarsus, 1.0 mm. Second patella and tibia, 2.7 mm; third, 1.1 mm; fourth, 2.4 mm.

Male. Male lighter colored than female. Diameter of posterior eyes 0.8 diameters of anterior medians. Anterior lateral eyes 0.6 diameters of anterior medians. Anterior median eyes their diameter apart, about 1.5 from laterals. Posterior median eyes about two diameters apart, about 1.8 from laterals (Figs. 41, 42). The chelicerae are not long, but the guide tooth has shifted anteriorly; the main tooth is the biggest (Figs. 41, 42). The base of the fang is attached to an area that seems narrow and projecting (Fig. 42). Total length, 3.8 mm. Carapace, 1.4 mm long, 0.9 mm wide. First femur, 3.1 mm; patella and tibia, 3.4 mm; metatarsus, 3.2 mm; tarsus, 0.9 mm. Second patella and tibia, 1.9 mm; third, 0.8 mm; fourth, 1.7 mm.

Diagnosis. Tetragnatha earmra has the lateral eyes closer together than the medians, and on a tubercle; there are large black rings around the eyes (Figs. 36, 41, 42).

[2] The exact location of Earmra South East Island could not be located in Everglades National Park. To avoid a name change, if Earmra turns out to be a misspelling, the name is considered an arbitrary combination of letters.

Plate 6. *Tetragnatha* male, left palpi; scanning electron micrographs of conductors and their tips; a–f, *T. versicolor*, compare to Figs. 98, 104–109. a, b, (Georgia); c, (Virginia), d, (Rhode Island); e, (Michigan); f, (California). g, *T. viridis*, compare to Fig. 119. h, i, *T. laboriosa*, compare to Fig. 128. *Scale lines.* 0.05 mm.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Like the larger *T. guatemalensis*, the paracymbium of the male has a distal bent finger (Fig. 44), but the tip of the conductor (Plate 5c; Fig. 45) appears twisted quite differently from that of *T. guatemalensis*.

The female has smaller chelicerae (Figs. 35, 36) than those of *T. guatemalensis*. There are two seminal receptacles, one behind the other on each side: one is lighter, ventral, pear-shaped and the other is darker, dorsal, more angular (Fig. 39). The seminal receptacles of *T. guatemalensis* are more elongate.

Paratypes. Florida. Everglades National Park: Paradise Key, 29 March 1951, ♂ (J. Vockeroth, CNC); Pineland Trail, 21 June 1964, ♀ (K. J. Stone, FSCA) (Map 2).

Tetragnatha guatemalensis O. P.-Cambridge

Plate 5d; Figures 46–55; Map 2

Tetragnatha guatemalensis O. P.-Cambridge, 1889, Biologia Centrali-Americana, Araneidea, 1: 8, pl. 2, figs. 6, 7, ♀, ♂. Male lectotype here designated from Guatemala [Cahabon or Laguna de los Coheteros near Cobán] in the British Museum, Natural History, examined. F. P.-Cambridge, 1903, Biologia Centrali-Americana, Araneidea, 2: 431, pl. 40, figs 12, 13, ♀, ♂. Chickering, 1959, Bull. Mus. Comp. Zool., 119: 482, figs. 13–21, ♀, ♂. Bonnet, 1959, Bibliographia Araneorum, 2: 4334.

Tetragnatha banksi McCook, 1893, American Spiders, 3: 262, pl. 25, fig. 6, pl. 28, fig. 4, ♂. Types from Florida and Wisconsin in the Academy of Natural Sciences, Philadelphia, lost.

Tetragnatha intermedia Banks, 1898, Proc. California Acad. Sci., ser. 3, 1: 247, pl. 15, fig. 14, ♂. One female, two male syntypes from Tepic, Mexico in the Museum of Comparative Zoology, examined, NEW SYNONYMY.

Tetragnatha seneca Seeley, 1928, Bull. New York State Mus., 178: 134, pl. 4, figs. 44–48, ♀, ♂. Male, female syntypes from Lodi Landing, Seneca Lake, New York in the American Museum of Natural History, examined. Kaston, 1948, Bull. Connecticut Geol. Natur. Hist. Surv., 70: 271, fig. 872, ♀. Bonnet, 1959, Bibliographia Araneorum, 2: 4355.

Tetragnatha laudativa Gertsch and Mulaik, 1936, Amer. Mus. Novitates, no. 863: 15, fig. 33, ♂ (only). Male holotype from Kingsville, Texas in the American Museum of Natural History, examined. NEW SYNONYMY.

Variation. The male chelicerae are at times as long as the carapace, sometimes shorter. Total length of females, 5.4 to 11.5 mm; males, 5.2 to 10.2 mm.

Diagnosis. This species has the lateral eyes always closer together than the medians and has a variable amount of dusky gray to black markings.

The male can readily be separated from that of other species except *T. earmra* by the presence of a finger extending from the tip of the palpal paracymbium (Figs. 53, 54); from *T. earmra* by the narrow lateral (in ventral view) extension on the tip of the conductor, straight or convex laterally (Plate 5d; Fig. 55). In contrast, that of *T. earmra* is concave laterally.

The female can only be separated from *Tetragnatha versicolor* and *T. dearmata* by examining the seminal receptacles: each member of the pair is oval, paraxial in position; one is dorsal and slightly to the side of the other (Fig. 50). The seminal receptacles are longer (Fig. 50) than the similar but more spherical ones of *T. earmra*. *Tetragnatha guatemalensis* has longer chelicerae (Figs. 46, 47) than *T. earmra*.

Natural History. Specimens have been collected from herbs; vegetation along marsh trail; sumac (*Rhus*) foliage and red pine (*Pinus resinosa*) in Ontario; sweeping honeysuckle (*Lonicera*) in West Virginia; and pine trees and web along grassy lakeshore in Wisconsin. In Florida specimens have been collected from weeds bordering streams; Australian

Plate 7. *Tetragnatha* male, left palpi: scanning electron micrographs of conductors and their tips; a, *T. pallescens*, compare to Fig. 139. b, c, *T. caudata*, compare to Fig. 148. d, *T. straminea*, compare to Fig. 157. e, f, *T. shoshone*, compare to Fig. 166. g, h, *T. branda*, compare to Fig. 175. i, *T. vermiformis*, compare to Fig. 184. *Scale lines.* 0.05 mm.

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pine (*Casuarina*); garden vegetation; tangerine tree; orange grove; and citrus grove. All these habitats were probably near the edge of rivers, lakes, and other water.

Distribution. Nova Scotia, Minnesota, Kansas, New Mexico, Southern California, south to Panama, Cuba, Jamaica. Border records are: Annapolis Royal, Nova Scotia, 1 Aug. 1971, ♂ (C. D. Dondale); Rocky Point, Lake of the Woods Co., Minnesota, ♂ (B. Cutler); Meade County State Park, Kansas, ♀, ♂ (W. Ivie); Bluewater Lake, 4 Sept. 1941, ♀ (W. Ivie); Sabino Canyon, Pima Co., Arizona, Sept. 1952, ♂; San Diego Co., California (several records) (Map 2).

Tetragnatha extensa (Linnaeus)
Plate 5e; Figures 56–64; Map 2

Aranea extensa Linnaeus, 1758, Systema Naturae, 10th ed., p. 621. Specimens from Sweden.

Tetragnatha extensa:—Tullgren, 1947, Entomol. Tidskr., 68: 130, figs. 1, 2, 7, 8, 16, 17, 19, 20, ♀, ♂. Locket and Millidge, 1953, British Spiders, 2: 100, figs. 64a, b, 66a, 67a, 68a, 69b, ♀, ♂. Wiehle, 1963, Tierwelt Deutschlands, 49: 12, fig. 5, web, figs. 13–19, ♀, ♂, egg-sac. Bonnet, 1959, Bibliographia Araneorum, 2: 4323 (in part only).

Tetragnatha manitoba Chamberlin and Ivie, 1942, Bull. Univ. Utah, biol. ser., 7(1): 61, figs. 153–158, ♀, ♂. Male holotype from Churchill, Manitoba in the American Museum of Natural History, examined.

Tetragnatha rusticana Chickering, 1959, Bull. Mus. Comp. Zool., 119: 489, figs. 36–40, ♀, ♂. Male holotype from Bay County, Michigan in the Museum of Comparative Zoology, examined. NEW SYNONYMY.

Note. Most American citations to the name *T. extensa* are misidentifications and actually refer to *T. versicolor.*

Variation. The female fang may have a cusp on its base (Fig. 57), or this may be absent. The distal tooth on the posterior margin of the chelicerae of females may be asymmetrical or may have a cusp. There may be a diastema behind this tooth, or this may be absent. One female examined from Colorado had one on one side, not on the other. Total length of females, 5.8 to 8.7 mm; males, 4.3 to 7.6 mm.

Diagnosis. The lateral eyes are almost as far apart as the medians (Figs. 57, 62). The male has the chelicerae slightly shorter than the length of the carapace (Fig. 61), the female considerably shorter (Fig. 56).

The male can readily be separated from *T. versicolor, T. shoshone,* and other North American species by the tip of the conductor, which is sclerotized laterally with the tiny tip pointed laterally toward the paracymbium (Plate 5e; Figs. 63, 64).

The female generally has a black sternum. The dorsum of the abdomen is silvery; the venter of the abdomen has a black band bordered on each side by a narrower, bright silver band. The posterior seminal receptacles of each pair are longer than the anterior and in a transverse position (Figs. 58, 60).

Natural History. This species has been collected sweeping the understory of aspen woods in British Columbia and Colorado, and also in wet meadows in Mon-

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Figures 16–22. Morphology of *Tetragnatha laboriosa.* 16. Sternum, labium, coxae, and endites of male. 17. Left femora of female, legs one and four, showing trichobothria, prolateral. 18–22. Male. 18–20. Left palpus, expanded. 18. Cymbium and paracymbium, lateral. 19. Subventral. 20. Mesal. 21. Posterior median eyes. 22. Left lateral eyes.

Figures 23–34. *Tetragnatha nitens* (Audouin). 23–29. Female. 23. Lateral, without legs. 24. Chelicerae and eye region. 25. Left chelicera from below. 26–29. Genital area. 26. Ventral. 27. Dorsal. 28. Ventral, cleared. 29. Left seminal receptacle, ventral. 30–34. Male. 30. Lateral. 31. Chelicerae and eye region. 32–34. Left palpus. 32. Ventral. 33. Lateral. 34. Conductor and embolus, ventral, and conductor tip, mesal.

Scale lines. 0.1 mm; except Figs. 16, 17, 23–25, 30, 31, 1.0 mm.

Abbreviations. C, conductor; E, embolus; h, hematodocha; P, paracymbium; T, tegulum; Y, cymbium.

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tana, Wyoming, and Colorado. It occurs up to timberline in the Colorado Rocky Mountains, about 3000 m elevation.

Distribution. Circumboreal, south to Maine, New Hampshire, New York, Michigan; in Rocky Mountains south to Chiricahua Mts., in the West to Idaho and Washington (Map 2). The southernmost record is from Herb Martyr Dam, Chiricahua Mts., Cochise Co., Arizona, ♀, 1 Sept. 1956 (A. F. Archer).

Tetragnatha dearmata Thorell
Plate 5f, Figures 65–73; Map 2

Tetragnatha dearmata Thorell, 1873, Remarks on Synonyms of European Spiders, p. 462. Specimens from Sweden. Tullgren, 1947, Entomol. Tidskr., 68: 139, figs. 32–44, ♀, ♂. Wiehle, 1963, Tierwelt Deutschlands, 49: 41, figs. 65–74, ♀, ♂. Bonnet, 1959, Bibliographia Araneorum, 2: 4321. Holm, 1973, Zool. Scripta, 2: 98.

Tetragnatha harrodi Levi, 1951, Amer. Mus. Novitates, no. 1501: 17, figs. 32–37, ♂. Male holotype from Harrowell, Prince Edward County, Ontario in the American Museum of Natural History. Chickering, 1959, Bull. Mus. Comp. Zool., 119: 484, figs. 22–25, ♀, ♂. NEW SYNONYMY.

Variation. Total length of females, 5.2 to 10.0 mm; total length of males, 5.9 to 6.8 mm.

Diagnosis. The lateral eyes are always much closer together than the medians (Figs. 66, 71).

Male *Tetragnatha dearmata* can be confused with *T. elongata*. However, the chelicerae of *T. dearmata* are shorter than the carapace (Fig. 70); *T. dearmata* lacks the first large (main) tooth on the anterior margin, and the tooth closest to the base of the fang is larger (Fig. 71). The similar European *T. montana* male has a large main tooth. The tibia of the palpus is shorter than the cymbium (Fig. 72). Unlike that of *T. elongata*, the middle of the conductor appears to have a thin fold; there is no basal, lateral, transparent shield on the conductor; and the tip of the conductor is a pennant, bent about 45° (Plate 5f; Figs. 72, 73).

The female is separated from *T. elongata* by the smaller chelicerae with fewer teeth (Figs. 65, 66), and from all *Tetragnatha* species by the doubled-up, U-shaped posterior lateral seminal receptacles (Fig. 69). Both margins of the silver streak on sides of the abdomen are wavy (Fig. 65).

Natural History. Specimens have been collected from white spruce in Northwest Territories; trees in New Brunswick; shrubs, tall grasses in a swamp, sweeping grass and forest, and a cottage in Ontario.

Distribution. Northern Eurasia, Alaska to northern states (Map 2). The southernmost localities are Trenton Falls, New York; Point Comfort, Winnebago Co., Wisconsin; Saint Peters, Nicollet Co., Minnesota; and near Forked Lake, Eagletown, McCurtain Co., Oklahoma, ♂ without date (Map 2).

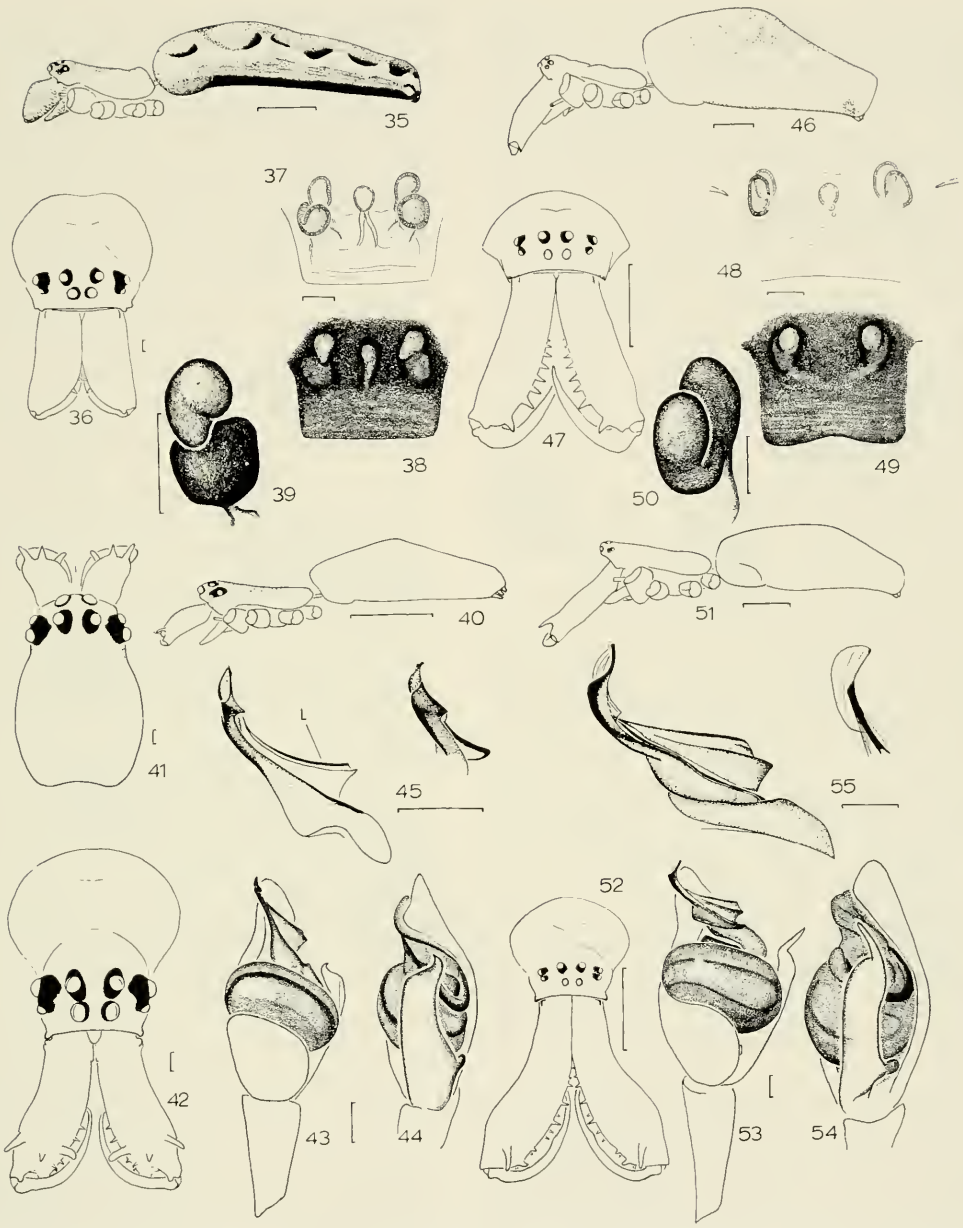
Tetragnatha elongata Walckenaer
Plates 5g–i; Figures 74–89; Map 3

Tetragnatha elongata Walckenaer, 1805, Tableau des Aranéides, p. 69. Name for Bosc manuscript fig. 5, ♀, "*Aranea gibba*" from the Carolinas. Photocopy in the Museum of Comparative Zoology, examined. Male neotype from Raleigh, North Carolina in garden, 21 to 31 August 1944 (C. S. Brimley) in the Museum of Comparative Zoology, here designated. Seeley, 1928, Bull. New York State Mus., 278: 109, pl. 1, figs. 11–13, pl. 2, figs. 14–16, ♀, ♂. Comstock, 1940, Spider Book, rev. ed., p. 425, figs. 424, 425, ♀, ♂. Roewer, 1942, Katalog der Araneae, 1: 992. Kaston, 1948, Bull. Connecticut Geol. Natur. Hist. Surv., 70: 270, figs. 853, 854, 865, 867, ♀, ♂. Bonnet, 1959, Bibliographia Araneorum, 2: 4322. Chickering, 1959, Bull. Mus. Comp. Zool., 119: 480, figs. 9–12, ♀, ♂.

Tetragnatha grallator Hentz, 1850, J. Boston Soc. Natur. Hist., 6: 26, pl. 4, figs. 1, 2, ♀, ♂. Syntypes from Pennsylvania, North and South Carolina, Alabama, destroyed.

Variation. Total length of females, 8.2 to 13.2 mm; of males, 4.8 to 10.5 mm. The smallest individuals are from the northern states, the largest from Texas. The tibia of the palpus is usually longer than the cymbium, occasionally shorter. Chelicerae from large and small specimens are illustrated by Figures 83–89.

Diagnosis. This species has the lateral eyes closer together than the medians, and both sexes have long chelicerae (Figs. 74, 75, 79, 80).



Figures 35–45. *Tetragnatha earmra* n. sp. 35–39. Female. 35. Lateral. 36. Chelicerae and eye region. 37–39. Genital area. 37. Dorsal. 38. Ventral, cleared. 39. Left seminal receptacles, ventral. 40–45. Male. 40. Lateral. 41. Carapace and chelicerae. 42. Chelicerae and eye region. 43–45. Left palpus. 43. Ventral. 44. Lateral. 45. Conductor, ventral, and conductor tip, mesal.

Figures 46–55. *Tetragnatha guatemalensis* O. P.-Cambridge. 46–50. Female. 46. Lateral. 47. Chelicerae and eye region. 48–50. Genital area. 48. Dorsal view. 49. Ventral, cleared. 50. Left seminal receptacles, ventral. 51–55. Male. 51. Lateral. 52. Chelicerae and eye region. 53–55. Palpus. 53. Ventral. 54. Lateral. 55. Conductor, ventral, and tip of conductor, mesal.

Scale lines. 0.1 mm; except Figs. 35, 40, 46, 47, 51, 52, 1.0 mm.

Abbreviations. L, pleats of conductor (Fig. 45).

The male is easily recognized by the conductor, which tapers evenly to its tip (Fig. 82) and terminates in a minute hook (Plate 5i). The distal third of the conductor is convex laterally, especially noticeable when viewed from slightly ventrolaterally. The tip bends toward the cymbium. There are usually three, sometimes two, pleats, and the base of the conductor has a transparent shield (Figs. 82, 88, 89). The conductor tip (Plate 5g) is much smaller than that of *T. straminea*. The palpus in ventral view can be confused with that of *T. dearmata*, but it lacks the dorsal extension of the tip. Unlike *Tetragnatha versicolor*, the male chelicerae are almost always longer than the carapace (Figs. 79, 84–87), and the recurved hook at the tip of the conductor is minute (Plate 5g–i; Fig. 82).

The female can readily be separated from other species: the chelicerae usually are at least equal to or greater than carapace length, usually with a lateral cusp outside near base of fang (Figs. 74, 75, 83). Unlike all other North American species, the median of each pair of seminal receptacles is longer than twice the width, and placed paraxial in the abdomen, parallel to each other (Figs. 76–78).

Natural History. The large, nearly horizontal (sometimes vertical) webs are placed over small streams or other running water, often in woods or shaded branches. The web has 4 to 5 turns outside of the hub, a free space, and 30 to 40 spirals.

Distribution. Eastern North American from New Brunswick, Quebec, Manitoba south to Cuba, Jamaica, central Mexico. Uncommon in Western states. Western records are: Salmon Arm and Wellington, British Columbia; northeast of Fruitland and Notus, Idaho; in Washington, Silver Lake, Cowlitz Co., Chase Lake, King Co., and Seattle; Eugene, Philomath, and Corvallis, Oregon; Monterey, California; and Sierra Laguna, Baja California (Map 3).

Tetragnatha versicolor Walckenaer
Plates 3, 6a–f; Figures 90–109; Map 3

Tetragnatha versicolor Walckenaer, 1841, Histoire Naturelle des Insectes Aptères, 2:215. Name given to Abbott's illustration of Georgian spiders, p. 20, fig. 231, ♀ and p. 37, fig. 466, ♀. Photocopy in the Museum of Comparative Zoology, examined. Male neotype from Bar-M Ranch, south of Boston, Thomas Co., Georgia, 4 April 1973 (W. T. Sedgwick) in the Museum of Comparative Zoology here designated. Kaston, 1948, Bull. Connecticut Geol. Natur. Hist. Surv., 70: 270, figs. 852, 862–864, ♀, ♂. Chickering, 1959, Bull. Mus. Comp. Zool., 119: 497, figs. 53–57, ♀, ♂.

Tetragnatha convexa Banks, 1898, Proc. California Acad. Sci., ser. 3, 1: 247. "Several specimens from San José del Cabo" Baja California in the California Academy of Sciences, destroyed in the California earthquake of 1906.

Tetragnatha extensa:—Seeley, 1928, Bull. New York State Mus., 278: 113, figs. 17–20, ♀, ♂. Comstock, 1940, Spider Book, rev. ed., p. 425. Bonnet, 1959, Bibliographia Araneorum, 2: 4323 (in part only). Not *T. extensa* Linnaeus.

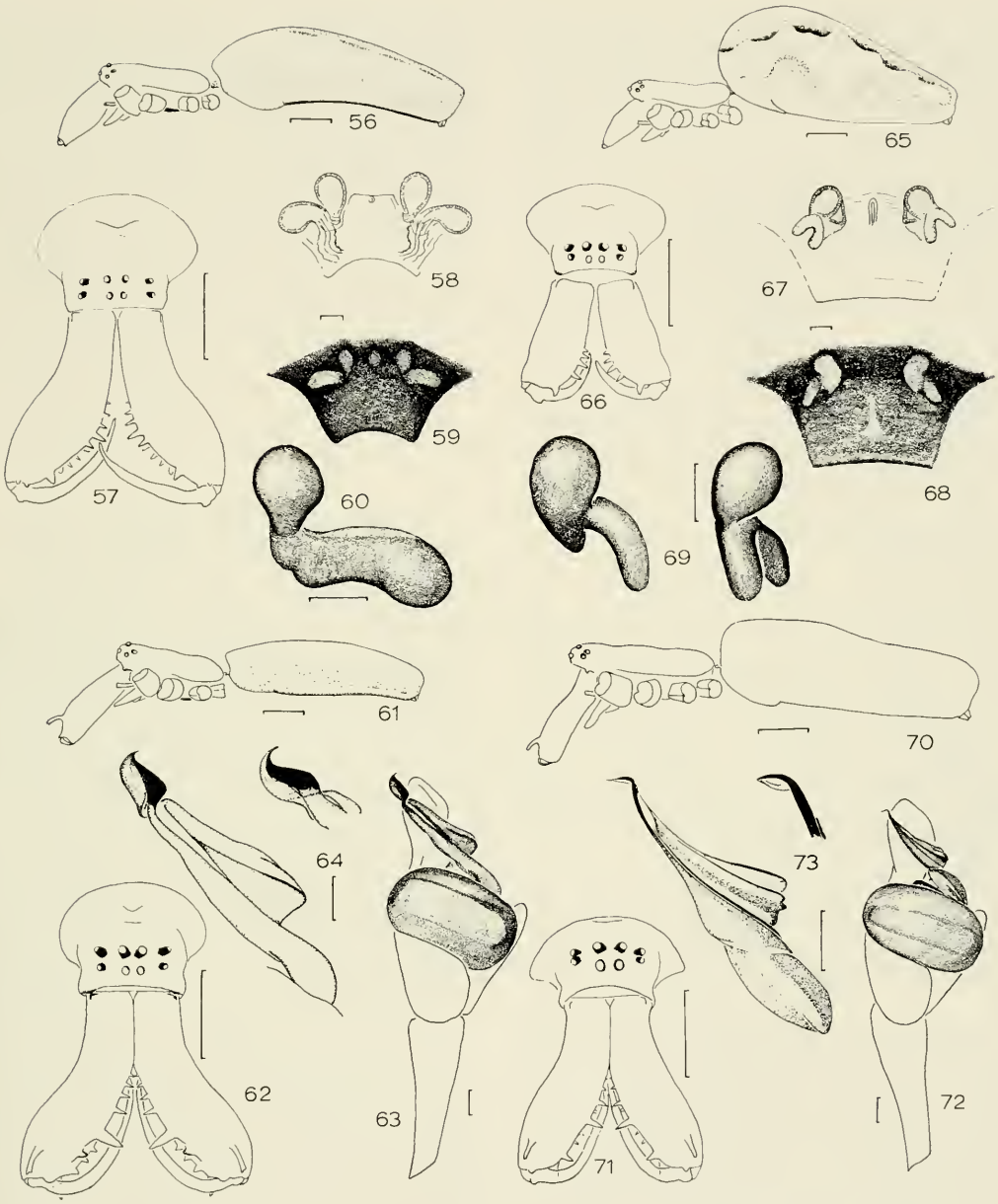
Tetragnatha limnocharis Seeley, 1928, Bull. New York State Mus., 278: 129, figs. 32–35, ♀, ♂. Male lectotype here designated from Nixon's Hammock, Okefenokee Swamp, Georgia in the American Museum of Natural History, examined. NEW SYNONYMY.

Tetragnatha munda Chamberlin and Gertsch, 1929, J. Ent. Zool., 21: 103, pl. 4, figs. 41–45, ♀, ♂. Male holotype from Clear Lake, California, in the American Museum of Natural History, examined. NEW SYNONYMY.

Tetragnatha marianna Archer, 1940, Paper Alabama Mus. Natur. Hist., 14: 20, pl. 1, fig. 1, ♂. Male holotype from Randon's Creek, Monroe Co., Alabama in the American Museum of Natural History, examined. NEW SYNONYMY.

Note. The Museum of Comparative Zoology collection has one male of *T. convexa* from Sierra Laguna, Baja California, N. Banks collection; the labels are in A.M. Chickering's handwriting. I am uncertain if this is a syntype of *T. convexa*.

Variation. This is a variable species. The abdominal patterns vary from completely silver to contrasting paired dorsal markings (Fig. 90). The base of the conductor of the palpus has at times a distinct transverse fold in the middle (Figs. 98, 104), but often this break is not visible. The tip of the conductor in western and northern specimens is sclerotized and



Figures 56–64. *Tetragnatha extensa* (Linnaeus). 56–60. Female. 56. Lateral. 57. Chelicerae and eye region. 58–60. Genital area. 58. Dorsal. 59. Ventral, cleared. 60. Left seminal receptacle, ventral. 61–64. Male. 61. Lateral. 62. Chelicerae and eye region. 63, 64. Left palpus. 63. Ventral. 64. Conductor, ventral, and tip, mesal.

Figures 65–73. *Tetragnatha dearmata* Thorell. 65–69. Female. 65. Lateral. 66. Chelicerae and eye region. 67–69. Genital area. 67. Dorsal. 68. Ventral, cleared. 69. Left seminal receptacles, ventrolateral and lateral. 70–73. Male. 70. Lateral. 71. Chelicerae and eye region. 72, 73. Palpus. 72. Ventral. 73. Conductor, ventral, and tip, mesal.

Scale lines. 0.1 mm; except Figs. 56, 57, 61, 62, 65, 66, 70, 71, 1.0 mm.

dark (Fig. 98); in southeastern specimens it is usually white (Figs. 104–109). Those with light tips for a while were considered a separate species since there were also differences in shape. But in examining a light-tipped specimen and a dark-tipped one collected together from Ontario, and a few dark-tipped ones from the South, I found that the differences were in degree of sclerotization; there are no consistent differences in shape (Plates 6a–f).

The tibia of the palpus is often longer than the cymbium in southeastern specimens; others from the same area have the tibia shorter than the cymbium.

One collection from Centreville, Wilkinson County, Mississippi, January to July 1944 (A. F. Archer) has the lateral eyes separated by the same distance as the medians.

Total length of females, 5.4 to 13.3 mm; total length of males, 4.3 to 9.2 mm. The largest specimens are from California, some of the smallest from the Everglades region in Florida.

The neotype and the original specimens illustrated by Abbot come from Georgia, where males have a lightly sclerotized conductor tip.

Diagnosis. This species has the lateral eyes closer to each other than the medians (Figs. 91, 96), and some dusky markings on cephalothorax and abdomen (Fig. 90).

The male can be separated from other species by the recurved tip of the conductor, pointing proximally; there is a slight swelling at the base of the tip (Plate 6a–f; Fig. 98). The male can be separated from *T. elongata* by the chelicerae, usually shorter than the carapace length (Figs. 95, 96). Males have been confused with *T. viridis*. *Tetragnatha versicolor* is never green, as is *T. viridis*; the lateral eyes in *T. versicolor* are closer together than the medians, in *T. viridis* as far apart as the medians.

The female has two seminal receptacles on each side, separated; the members of each pair are less than their diameter apart (Figs. 92–94). The placement and shape are different from those of other *Tetragnatha* species with lateral eyes closer together than medians.

Natural History. Specimens have been collected from mixed coniferous forests; spruce forests; flood plain forests, deciduous trees; grasses along edges of fields, always near water; and various species of trees and shrubs, including aspens in Wyoming, oranges in Florida, and sweeping sagebrush (*Artemia* sp.) in Colorado.

Distribution. Alaska to Nicaragua and Cuba (Map 3).

Tetragnatha viridis Walckenaer
Plates 3, 6g; Figures 110–119; Map 3

Tetragnatha viridis Walckenaer, 1841, Histoire Naturelle des Insectes Aptères, 2:216. Name given to fig. 236, ♀, p. 20 and fig. 471, ♀, p. 37 of Abott's manuscript of Georgian spiders. Photocopies in the Museum of Comparative Zoology, examined. Male neotype from Brier Creek, 7 mi. north of Sylvania, Screven County, Georgia, 12 April 1943 (W. Ivie) in the American Museum of Natural History, here designated. Kaston, 1948, Bull. Connecticut Geol. Natur. Hist. Surv., 70: 272.

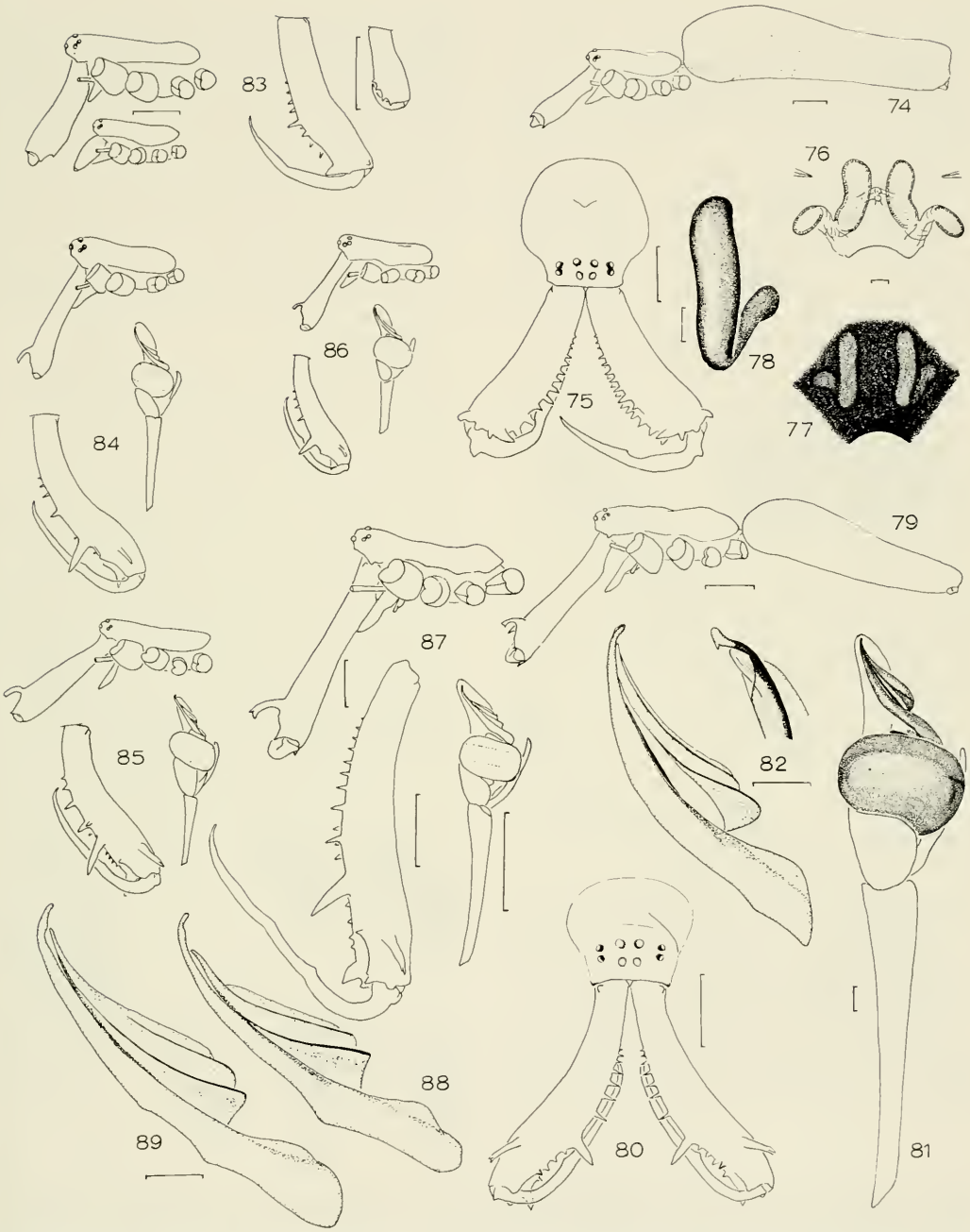
Tetragnatha pinicola Emerton, 1915, Trans. Connecticut Acad. Sci., 20: 139, figs. 7a, b, ♀, ♂. One male, four female syntypes from Nantucket, Massachusetts, in the Museum of Comparative Zoology, examined. Not *T. pinicola* L. Koch, 1870.

Tetragnatha pinea Seeley, 1928, Bull. New York State Mus., 278: 133, figs. 21–24, ♀, ♂. New name for *T. pinicola* Emerton preoccupied by L. Koch. Bonnet, 1959, Bibliographia Araneorum, 2: 4351.

Note. Chickering determined *T. viridis* specimens in collections as *T. versicolor*.

Variation. Some specimens are all green, some are partly reddish. A green juvenile from Massachusetts turned into an adult male after two molts (in a vial), with carapace greenish on sides; sternum reddish; legs light brown with red spots; dorsum of abdomen with a wide longitudinal red band having parallel white sides; sides of abdomen dark green; venter silvery.

The green and red color fade rapidly in alcohol preserving fluid. Total length of



Figures 74–89. *Tetragnatha elongata* Walckenaer. 74–78. Female. 74. Lateral. 75. Chelicerae and eye region. 76–78. Genital area. 76. Dorsal. 77. Ventral, cleared. 78. Left seminal receptacles, ventral. 79–82, Male. 79. Lateral. 80. Chelicerae and eye region. 81, 82. Left palpus. 82. Conductor and embolus, ventral, and conductor tip, mesal. 83–89. *Variation.* 83. Carapace and left chelicera of two adult females collected together (Massachusetts). 84–87. Male carapace, left chelicera and left palpus. 84. (Massachusetts). 85. (Wisconsin). 86. (Washington state). 87. (Texas). 88, 89. Conductor, ventral. 88. (Wisconsin). 89. (Texas).

Scale lines. 0.1 mm; except Figs. 74, 75, 79, 80, 83–87, 1.0 mm.

females, 5.7 to 7.4 mm; total length of males, 4.4 to 6.7 mm.

Diagnosis. Faded, preserved specimens look like *T. laboriosa* but have genitalia like those of *T. versicolor*. The lateral eyes are about as far apart as the medians (Figs. 111, 117).

Specimens can be distinguished from *T. laboriosa* by the green or reddish color; in males by the similarity of the palpal conductor tip to that of *T. versicolor* (Plate 6g; Fig. 119); and in females by the seminal receptacles (Fig. 114).

This species can easily be distinguished from *T. versicolor*, which has similar genitalia, by the separated lateral eyes (Figs. 111, 117). These are farther apart than the medians in the male, as far apart as the medians in the female. Other distinguishing features are the green to red coloration, and the abdominal markings: bands with straight margins (Fig. 110) rather than the lobed gray markings on the dorsum of *T. versicolor*. *T. viridis* also differs from *T. laboriosa* and *T. versicolor* by the long macrosetae on the legs; those of the first tibia have a length 5 to 8 times the diameter of the tibia (Fig. 115).

The green coloration and long leg macrosetae make it possible to determine juveniles.

The only differences that could be found in the conductors of *T. viridis* and *T. versicolor* are in the pleats near the base at the lateral end: in *T. viridis* they look as though lifted up (Fig. 119).

Natural History. This species lives in pines, occasionally in other conifers, and is difficult to find since it rests appressed to the needles. It is also difficult to dislodge by sweeping or beating. In Massachusetts the species is common in pitch pine (*Pinus rigida*) in sandy areas of Cape Cod. In Massachusetts adults can be found from late May to early July. Juveniles are found later in the season, and they overwinter. This short season is unusual for *Tetragnatha*.

Distribution. New Brunswick to North Carolina along coastal pine forest, southeastern states to northern Florida, eastern Texas (Map 3).

Records. New Brunswick. Fredericton, 6–9 July 1970, ♀ in balsam fir (T. R. Renault). *Massachusetts.* Barnstable Co.: Chatham, South Chatham, Harwich, between Falmouth and Bourne, many specimens. Essex Co.: Essex 24 June 1878, pine trees, ♀, ♂ (J. H. Emerton). *Connecticut.* New Haven Co.: Mt. Carmel, 12 Sept. 1936, juv. (B. J. Kaston). *New Jersey.* Ocean Co.: Lakehurst, 13 May 1909, ♀, ♂. *North Carolina.* Pasquotank Co.: Elizabeth City, May 1900, ♂ (J. H. Emerton). *Georgia.* Thomas Co.: Bar-M Ranch, 28 April 1973, ♀ (G. B. Edwards). *Florida.* Jackson Co.: 30 mi. southeast of Marianna, 1 May 1933, ♀ (H. K. Wallace). Jefferson Co.: Monticello, 11 April 1968, ♀ (A. M. Chickering). Liberty Co.: Rock Bluff, 4 April 1927, ♂ (C. R. Crosby). *Alabama.* Lee Co.: Chewacla Creek State Park, April 1947, ♂ (A. F. Archer). Tuscaloosa Co.: Tuscaloosa, 13 April 1941, ♂ (A. F. Archer). *Arkansas.* Calhoun Co.: 5 Nov. 1964, juv. on pine (L. O. Warren). *Texas.* Harris Co.: 9 mi. west of Tomball, 5 Dec. 1968, juv. in freshly felled pine (E. Sabath).

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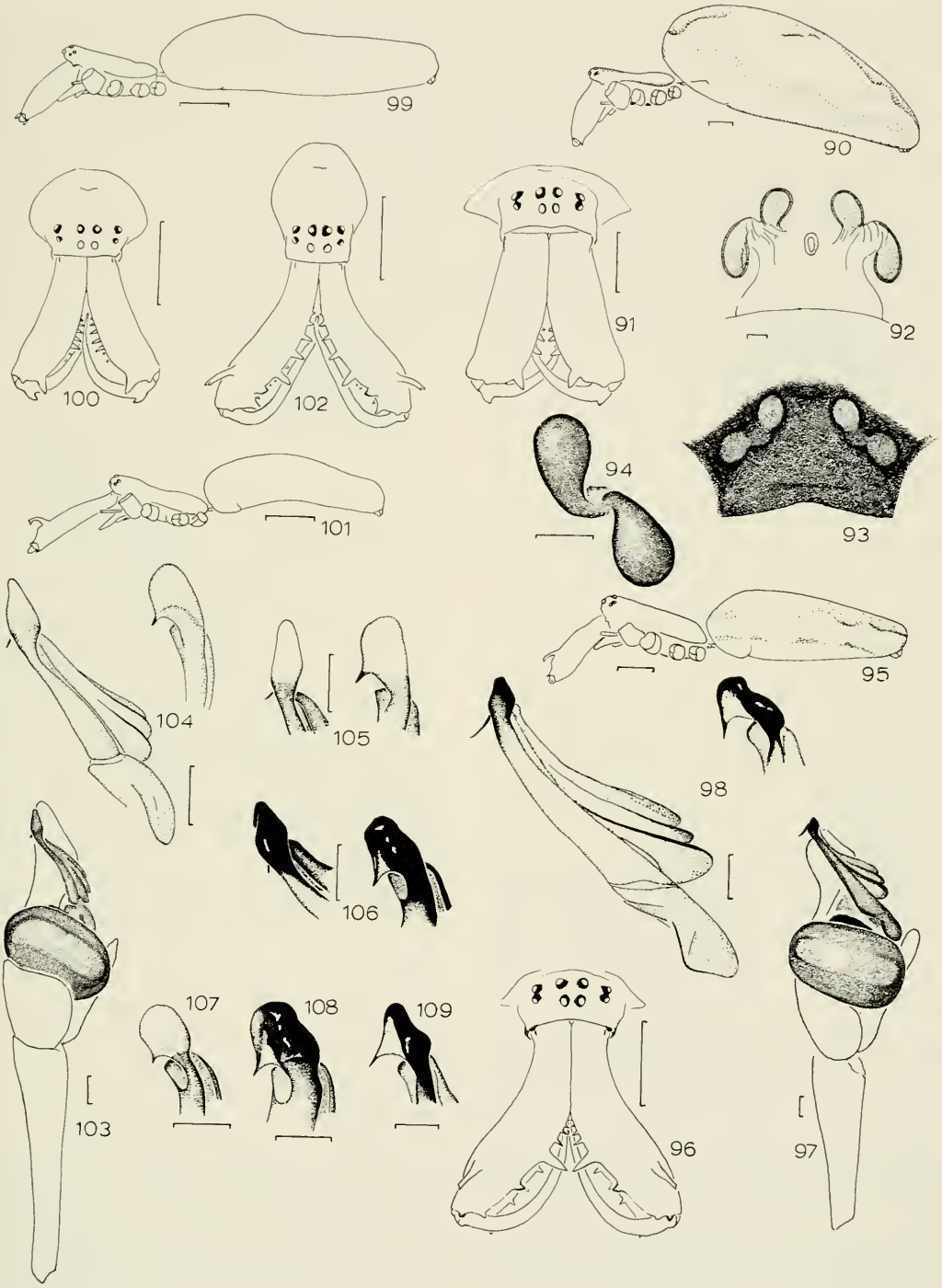
Figures 90–109. *Tetragnatha versicolor* Walckenaer. 90–94. Female (California except 94, Michigan). 90. Lateral. 91. Chelicerae and eye region. 92–94. Genital area. 92. Dorsal. 93, Ventral, cleared. 94. Left seminal receptacles, ventral. 95–98. Male (California). 95. Lateral. 96. Chelicerae and eye region. 97, 98. Left palpus. 97. Ventral. 98. Conductor, ventral, and tip, mesal. 99–109. *Variation.* 99, 100. Female (Florida). 99. Lateral. 100. Chelicerae and eye region. 101, 102. Male (Georgia). 101. Lateral. 102. Chelicerae and eye region. 103, 104. Palpus (Georgia). 103. Ventral. 104. Conductor, ventral, and tip, mesal. 105, 106. Conductor tips, ventral and mesal (both Oxford Mills, Ontario). 107–109. Conductor tips, mesal. 107. (New Brunswick). 108. (Neel Gap, Georgia). 109. (California).

Scale lines. 0.1 mm; except Figs. 90, 91, 95, 96, 99–102, 1.0 mm.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Tetragnatha laboriosa Hentz

Plate 6h, i; Figures 16–22, 120–128; Map 3

Tetragnatha laboriosa Hentz, 1850, J. Boston Soc. Natur. Hist., 6: 27, pl. 4, fig. 3, ♂. Specimens from United States, destroyed. Male neotype from Holliston, Massachusetts, 23 June 1929 (N. Banks) in the Museum of Comparative Zoology here designated. Seeley, 1928, Bull. New York State Mus., 278: 123, figs. 25–31, ♀, ♂. Comstock, 1940, Spider Book, rev. ed., p. 426. Roewer, 1942, Katalog der Araneae, 1: 992. Kaston, 1948, Bull. Connecticut Geol. Natur. Hist. Surv., 70: 269, figs. 850–851, 859–861, ♀, ♂. Chickering, 1959, Bull. Mus. Comp. Zool., 119: 486, figs. 26–30, ♀, ♂. Bonnet, 1959, Bibliographia Araneorum, 2: 4335.

Tetragnatha illinoiensis Keyserling, 1879, Verhandl. Zool. Bot. Gesell. Wien, 29: 318, pl. 4, fig. 18, ♀. Female from Illinois in the British Museum, Natural History, examined.

Tetragnatha numa Levi, 1955, Canadian Field Natur., 69: 37, figs. 19–23, ♀, ♂. Male holotype from Bowman Lake, Glacier National Park, Montana in the American Museum of Natural History, examined. NEW SYNONYMY.

Variation. The lateral eyes are usually as far apart as the medians, sometimes slightly closer together or very slightly farther apart. Occasionally there is a dark folium on the dorsum of the abdomen; the folium is usually more distinct posteriorly than anteriorly. Total length of females, 5.2 to 9.0 mm; total length of males, 3.8 to 7.4 mm.

Diagnosis. The lateral eyes are almost as far apart or as separate as the medians (Figs. 121, 126). Similar eye distances are also found in *T. extensa*, *T. shoshone*, and the green *T. viridis*. There is very little gray pigment on the body.

The male differs from other species by the bird head-shaped tip of the conductor (Plate 6i; Fig. 128); the tip is often slightly turned to point dorsally to the cymbium. The conductor is twisted near midway, and there are about two pleats, the proximal pleat lifted up away from the conductor (Plate 6h; Figs. 127, 128).

The female can only be separated from similar species by the seminal receptacles. Each pair has a large pouch between the anterior and posterior receptacles which partly hides the anterior receptacle in ventral view (Fig. 124). This is unlike that of any other species.

Natural History. Specimens have been found in grass, often dry fields some distance from water; in soybean fields in North Carolina; in cotton, sweet potato, and alfalfa fields in Arkansas; in tomatoes in California; in pasture in Texas; in high meadows to 3000 m elevation in Colorado; and in bog in New Brunswick. It has rarely been found in trees.

Distribution. Alaska to Panama (Map 3).

Tetragnatha pallescens F. P.-Cambridge

Plates 4, 7a; Figures 129–139; Map 4

Eugnatha pallida Banks, 1892, Proc. Acad. Natur. Sci. Philadelphia, p. 51, fig. 88, ♂. Two male and one female syntypes from Ithaca, New York in the Museum of Comparative Zoology, examined. Not *T. pallida* O. P.-Cambridge, 1889.

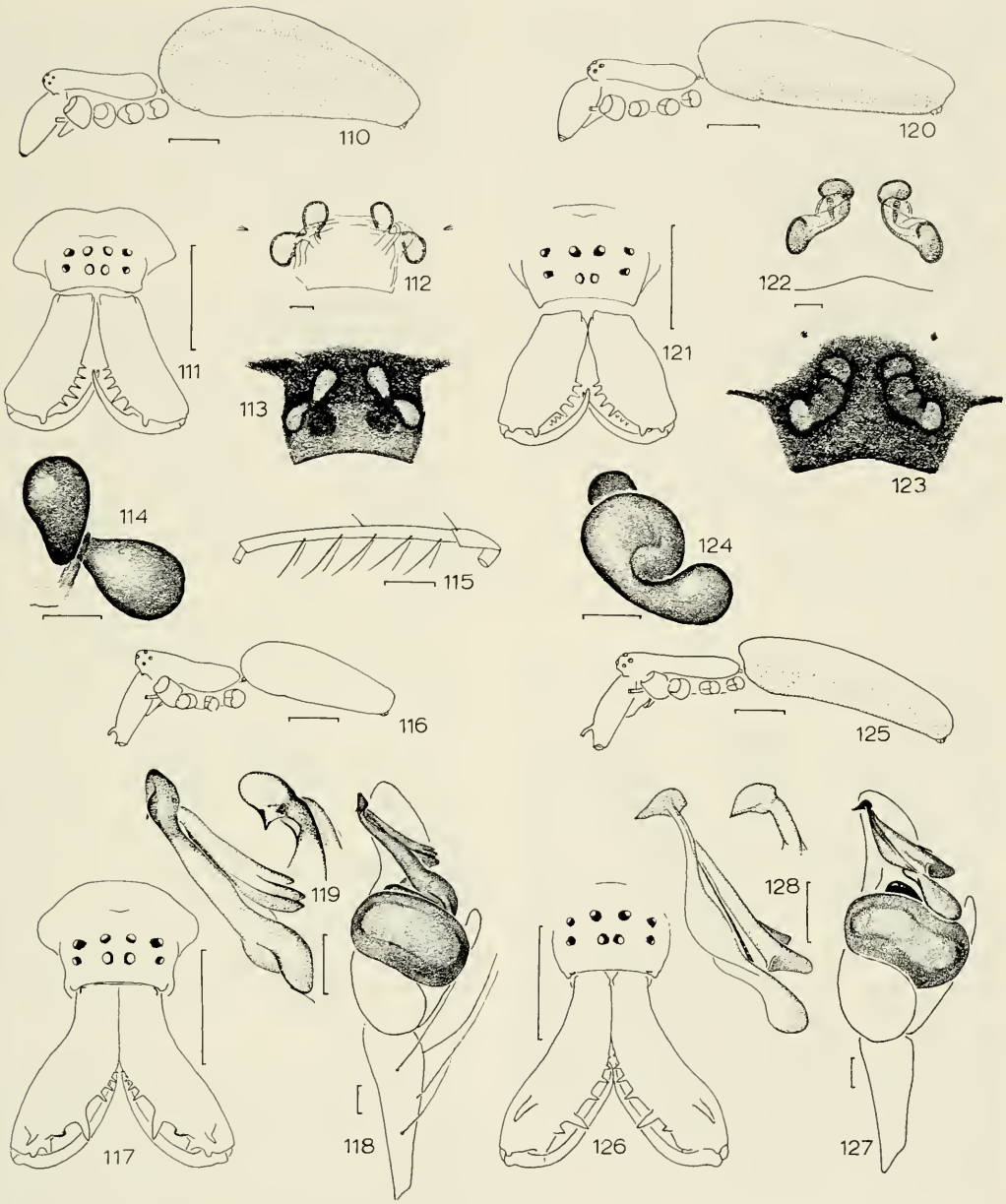
Tetragnatha pallescens F. P.-Cambridge, 1903, Biologia Centrali-Americana, Araneidea, 2: 436. New name for *T. pallida* Banks preoccupied by *T. pallida* O. P.-Cambridge. Seeley, 1928, Bull. New York State Mus., 278: 131, pl. 3, figs. 40–43, ♀, ♂. Comstock, 1940, Spider Book, rev. ed., p. 429. Roewer, 1942, Katalog der Araneae, 1:992. Kaston, 1948, Bull. Connecticut Geol. Natur. Hist. Surv., 70: 272, figs. 875–876, ♀, ♂. Chickering, 1959, Bull. Mus. Comp. Zool., 119:487, figs. 31–35, ♀, ♂. Bonnet, 1959, Bibliographia Araneorum, 2: 4350.

Eugnatha pallidula Banks, 1910, Bull. U.S. Natl. Mus., 72, p. 36. New name for *T. pallida* Banks, preoccupied by *T. pallida* O. P.-Cambridge.

Variation. Females may have either large or small chelicerae (Figs. 134, 135). Total length of females, 7.3 to 12.2 mm; males, 6.5 to 9.6 mm.

Diagnosis. The lateral eyes are farther apart than the medians (Figs. 130, 137). The abdomen is entirely covered with minute silvery spots, the spots least dense on the venter.

The male can be separated from other species having similar eye spacing by the conductor of the palpus: the lower surface of the proximal end is concave (Figs. 138, 139), and the tip has a bulge above



Figures 110–119. *Tetragnatha viridis* Emerton. 110–115. Female. 110. Lateral. 111. Chelicerae and eye region. 112–114. Genital area. 112. Dorsal. 113. Ventral, cleared. 114. Left seminal receptacles, ventral. 115. First left patella and tibia with macrosetae. 116–119. Male. 116. Lateral. 117. Chelicerae and eye region. 118, 119. Left palpus. 118. Ventral, 119, Conductor, ventral, and tip, mesal.

Figures 120–128. *Tetragnatha laboriosa* Hentz. 120–124. Female. 120. Lateral. 121. Chelicerae and eye region. 122–124. Genital area. 122. Dorsal. 123. Ventral, cleared. 124. Left seminal receptacles, ventral. 125–128. Male. 125. Lateral. 126. Chelicerae and eye region. 127, 128. Palpus. 127. Ventral. 128. Conductor with embolus, ventral, and conductor tip, mesal.

Scale lines. 0.1 mm; except Figs. 110, 111, 116, 117, 120, 121, 125, 126, 1.0 mm.

the neck (in ventral view) under the terminal hook (Plate 7a; Fig. 139). There is one pleat (Fig. 139).

The female is separated from *T. caudata*, *T. branda*, and *T. vermiformis* by the long, slender shape of the abdomen, lacking a tail (Fig. 129). Females are separated from *T. straminea* by the abdomen having silver sides (Fig. 129); there is no distinct line where the silver ends and the pigmentless area starts, but sometimes the dorsal silver grades into a less dense ventral silver area. Females can be confused with those of *T. laboriosa*, but *T. laboriosa* has some gray pigment on the sternum and venter of the abdomen, absent in *T. pallescens*. In the West Indies and Central America, where *T. straminea* does not occur, *Tetragnatha pallescens* may have a line on each side, above which there is silver and below which there are only scattered silver spots.

Females from the northern part of the range can be confused with those of *T. shoshone*. The seminal receptacles of each pair are more than their distance apart in *T. pallescens*, with the intermediate connection being a lobe (Fig. 133); in *T. shoshone* they are almost touching.

Natural History. Specimens have been collected from pine trees on Nantucket, Massachusetts, and sandflats and lake shore in Pennsylvania. In Florida the species has been found in parlor palm (*Chamaedorea erumpens*), mangroves, tall grasses, roadside weeds, vegetation along lakeshore and pond in waste fields. It has also been found in rice in Arkansas, and grasses in water in Texas.

Distribution. Southern Canada to Panama, West Indies (Map 4).

Tetragnatha caudata Emerton
Plate 7b, c; Figures 140–148; Map 4

Tetragnatha caudata Emerton, 1884, Trans. Connecticut Acad. Sci., 6: 335, pl. 39, figs. 16, 22, ♀. Penultimate instar female holotype in poor physical condition from Malden, Massachusetts in the Museum of Comparative Zoology, examined. Seeley, 1928, Bull. New York State Mus., 278: 107, figs. 5–10, ♀, ♂. Kaston, 1948, Bull. Connecticut Geol. Natur. Hist. Surv., 70: 273, figs. 873, 874, ♀. Chickering, 1959, Bull. Mus. Comp. Zool., 119: 479, figs. 1–8, ♀, ♂.

Tetragnatha lacerta:—Comstock, 1940, Spider Book, rev. ed., p. 429, fig. 428, ♀. Roewer, 1942, Katalog der Araneae, 1: 993.

Eucta lacerta:—Bonnet, 1956, Bibliographia Araneorum, 2: 1807.

Note. This species has often been referred to as *T. lacerta* Walckenaer. *Tetragnatha lacerta* is a doubtful name and has also been used for *Argyrodes fictilium* (Hentz), Theridiidae.

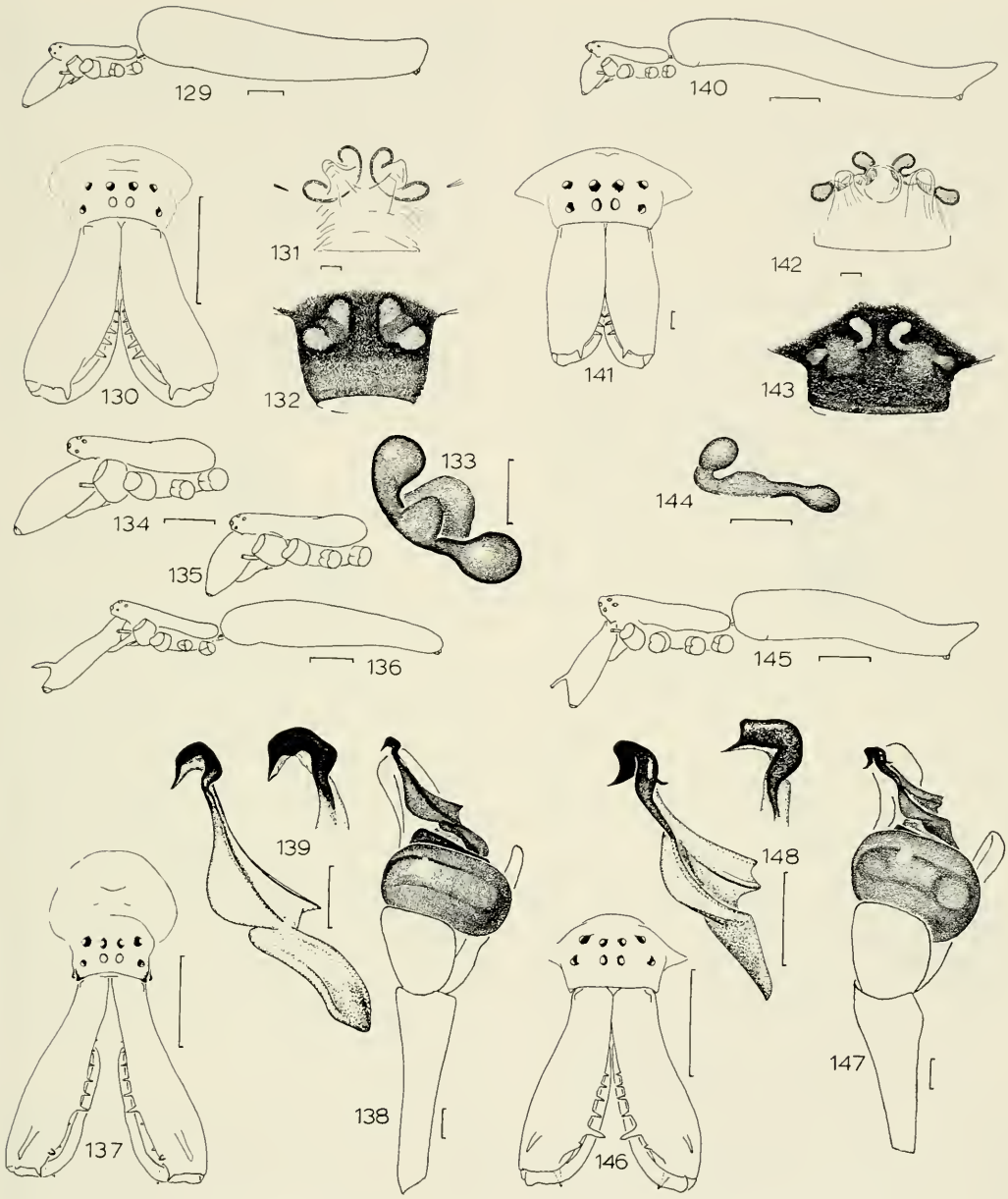
Variation. Tail length is quite variable, often very much longer than illustrated. Total length of females, 7.6 to 11.5 mm; of males, 5.7 to 8.9 mm. The lateral eyes are farther apart than the medians (Figs. 141–146).

Diagnosis. Both sexes are readily separated from other *Tetragnatha* species (except *T. branda*) by the presence of a tail behind the spinnerets (Figs. 140–145).

Tetragnatha caudata males have pleats on their conductor, and a hook on the tip of the conductor (Plate 7b, c; Fig. 148), both lacking in *T. branda*. In males the proximal end of the conductor is twisted below the pleats (Fig. 148); the distal hook faces mesally and points dorsally (Plate 7b; Fig. 148). At the base of the hook is a small spur seen in ventral view, absent in other species (Plate 7c; Fig. 147).

In females the seminal receptacles are relatively small, the anterior medians of each pair closer together than to the other member of the pair (Figs. 142–144). Those of *T. branda* are close to each other on each side. The abdomen is entirely silver; on the dorsum the silver spots are fused, whereas they are less dense in a longitudinal line on the venter.

Natural History. Specimens have been collected from bogs; marshes; weeds along canal; swamp grass; lakeshores;



Figures 129–139. *Tetragnatha pallescens* F. P.-Cambridge. 129–135. Female. 129. Lateral. 130. Chelicerae and eye region. 131–133. Genital area. 131. Dorsal. 132. Ventral, cleared. 133. Left seminal receptacles, ventral. 134, 135. Carapace and chelicera of mature females (Tamiami Trail, Dade Co., Florida). 136–139. Male. 136. Lateral. 137. Chelicerae and eye region. 138, 139. Left palpus. 138. Ventral. 139. Conductor, ventral, and tip, mesal.

Figures 140–148. *Tetragnatha caudata* Emerton. 140–144. Female. 140. Lateral. 141. Chelicerae and eye region. 142–144. Genital area. 142. Dorsal. 143. Ventral, cleared. 144. Left seminal receptacles, ventral. 145–148. Male. 145. Lateral. 146. Chelicerae and eye region. 147, 148, Palpus. 147. Ventral. 148. Conductor, ventral, and tip, mesal.

Scale lines. 0.1 mm; except Figs. 129, 130, 134–137, 140, 141, 145, 146, 1.0 mm.

and ponds. In the Everglades the species has been found in tall grass.

Distribution. From Great Slave Lake to Panama, Cuba; absent from southwestern United States (Map 4). The northernmost locality are juvenile specimens from 5 mi. SE of Fort Providence, 15 Aug. 1965 (J. and W. Ivie, AMNH).

Tetragnatha straminea Emerton
Plates 4, 7d; Figures 149–157; Map 4

Tetragnatha straminea Emerton, 1884, Trans. Connecticut Acad. Sci., 6: 335, pl. 39, figs. 15, 17, 20, 21, ♀, ♂. One male and two female syntypes from New Haven, Connecticut in the Museum of Comparative Zoology, examined. Seeley, 1928, Bull. New York State Mus., 278: 136, figs. 49–54, ♀, ♂. Roewer, 1942, Katalog der Araneae, 1: 994. Comstock, 1940, Spider Book, rev. ed., p. 428, fig. 427, ♀. Kaston, 1948, Bull. Connecticut Geol. Natur. Hist. Surv., 70: 271, figs. 855–856, 868–871, ♀, ♂. Chickering, 1959, Bull. Mus. Comp. Zool., 119: 494, figs. 41–46, ♀, ♂. Bonnet, 1959, Bibliographia Araneorum, 2: 4356.

Variation. Total length of females, 7.1 to 12.7 mm; total length of males, 5.7 to 10.1 mm.

Diagnosis. The lateral eyes are much farther apart than the medians. Only the dorsum of the abdomen is silver (Figs. 149, 150, 154, 155).

The male of *T. straminea* can be separated from the other four species having similar eye placement by the paddle-shaped tip of the conductor (Fig. 157). The conductor has a narrow neck just below the tip (Plate 7d; Figs. 156, 157), unlike that of the similar *T. shoshone.*

The females can be separated from *T. caudata, T. branda, T. vermiformis, T. shoshone,* and *T. pallescens* by several features of the abdomen. Unlike *T. caudata,* the long abdomen of *T. straminea* lacks a tail. Unlike *T. caudata, T. shoshone, T. vermiformis,* and *T. pallescens,* the upper, silvery half of each side is clearly delineated from the ventral half by a straight line. Also, the seminal receptacles are more variable in position than those of other species. Although they might be confused with those of *T. pallescens,* in *T. straminea* these structures are about their length apart (Fig. 153), nor is the connection swollen.

Natural History. Specimens have been collected from sweeping ferns and bogs in Ontario; sweeping honeysuckle (*Lonicera* sp.) in West Virginia; cedar bogs in Ohio; rocky gorges in New York; and bottomland forests and swamp foliage in Florida.

Distribution. Northern Alberta, Ontario, Utah, Florida, Cuba (Map 4). The northernmost collection came from Fort Murray, Alberta, July 1953, ♂ (G. E. Ball).

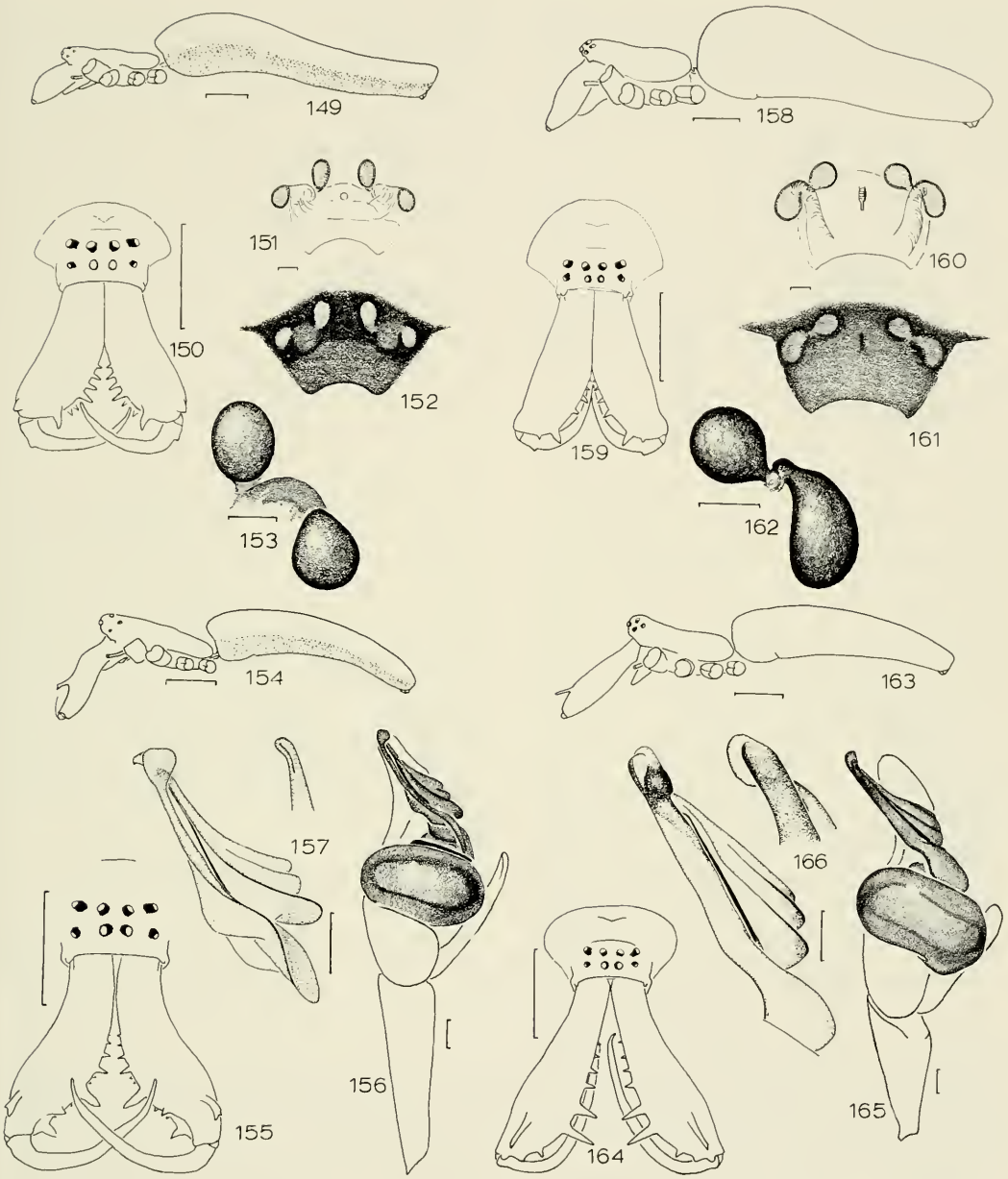
Tetragnatha shoshone new species
Plates 7e, f; Figures 158–166; Map 4

Holotype. Male from Laketown, Rich County, Utah, 30 July 1978 (G. F. Knowlton) in the Museum of Comparative Zoology. The name is a noun in apposition after the Indian tribe.

Description. Female. Carapace, sternum, legs yellowish. Abdomen evenly covered with tiny silver pigment spots all around, except for cardiac area and a narrow ventral band to spinnerets (Fig. 158). Eyes subequal in size, except for anterior laterals, 0.8 diameters of others. Laterals very slightly farther apart than medians (Fig. 159). Total length, 9.4 mm. Carapace, 2.6 mm long, 1.7 mm wide. First femur, 5.2 mm; patella and tibia, 6.0 mm; metatarsus, 5.2 mm; tarsus, 1.4 mm. Second patella and tibia, 3.9 mm; third, 1.9 mm; fourth, 4.0 mm.

Male coloration and eyes like female. Chelicerae as illustrated (Fig. 164). Total length, 6.8 mm. Carapace, 2.5 mm long, 1.4 mm wide. First femur, 5.8 mm; patella and tibia, 7.0 mm; metatarsus, 6.5 mm; tarsus, 1.8 mm. Second patella and tibia, 4.8 mm; third, 2.2 mm; fourth, 4.5 mm.

Variation. Canadian specimens have black pigment on the abdomen: those from Great Slave Lake, two pairs of black



Figures 149–157. *Tetragnatha straminea* Emerton. 149–153. Female. 149. Lateral. 150. Chelicerae and eye region. 151–153. Genital area. 151. Dorsal. 152. Ventral, cleared. 153. Left seminal receptacles, ventral. 154–157. Male. 154. Lateral. 155. Chelicerae and eye region. 156, 157. Left palpus. 156. Ventral. 157. Conductor with embolus, ventral, and tip, mesal.

Figures 158–166. *Tetragnatha shoshone* n. sp. 158–162. Female. 158. Lateral. 159. Chelicerae and eye region. 160–162. Genital area. 160. Dorsal. 161. Ventral, cleared. 162. Left seminal receptacles, ventral. 163–166. Male. 163. Lateral. 164. Chelicerae and eye region. 165, 166. Palpus. 165. Ventral. 166. Conductor with embolus, ventral, and tip, mesal.

Scale lines. 0.1 mm; except Figs. 149, 150, 154, 155, 158, 159, 163, 164, 1.0 mm.

patches; those from Ontario, wavy gray lines on the sides of the dorsum. The lateral eyes are a variable distance apart, always closer than those of *T. pallescens* and *T. straminea*. If close, the lateral eyes are separated about 1.3 times the distance of the medians.

Total length of females, 8.6 to 12.3 mm; total length of males, 5.4 to 8.8 mm. The smallest specimens are those from Utah and Idaho, the largest from the periphery of the range: Ontario and California.

Diagnosis. The lateral eyes are always slightly farther apart than the medians (Figs. 159, 164).

Although *Tetragnatha shoshone* can be confused with *T. extensa, T. laboriosa, T. pallescens,* and *T. straminea,* males can be separated by the shape of the conductor. *T. shoshone* lacks a mesally-facing beak as conductor tip (Plate 7f), present in *T. laboriosa* and *T. pallescens*. It also lacks the laterally facing, pointed tip of *T. extensa*; it has a wider neck below the conductor tip than does *T. straminea* (Plate 7e, f; Figs. 165, 166).

Females differ from *T. extensa* and *T. laboriosa* in having the lateral eyes slightly farther apart than the medians (Figs. 158, 159). *T. shoshone* can be distinguished from *T. pallescens* by the seminal receptacles: the posterior is larger than and almost touching the anterior (Fig. 162), whereas those of *T. pallescens* are some distance from each other and separated by a lobe of the ducts.

Natural History. This species has been collected sweeping vegetation near large lakes.

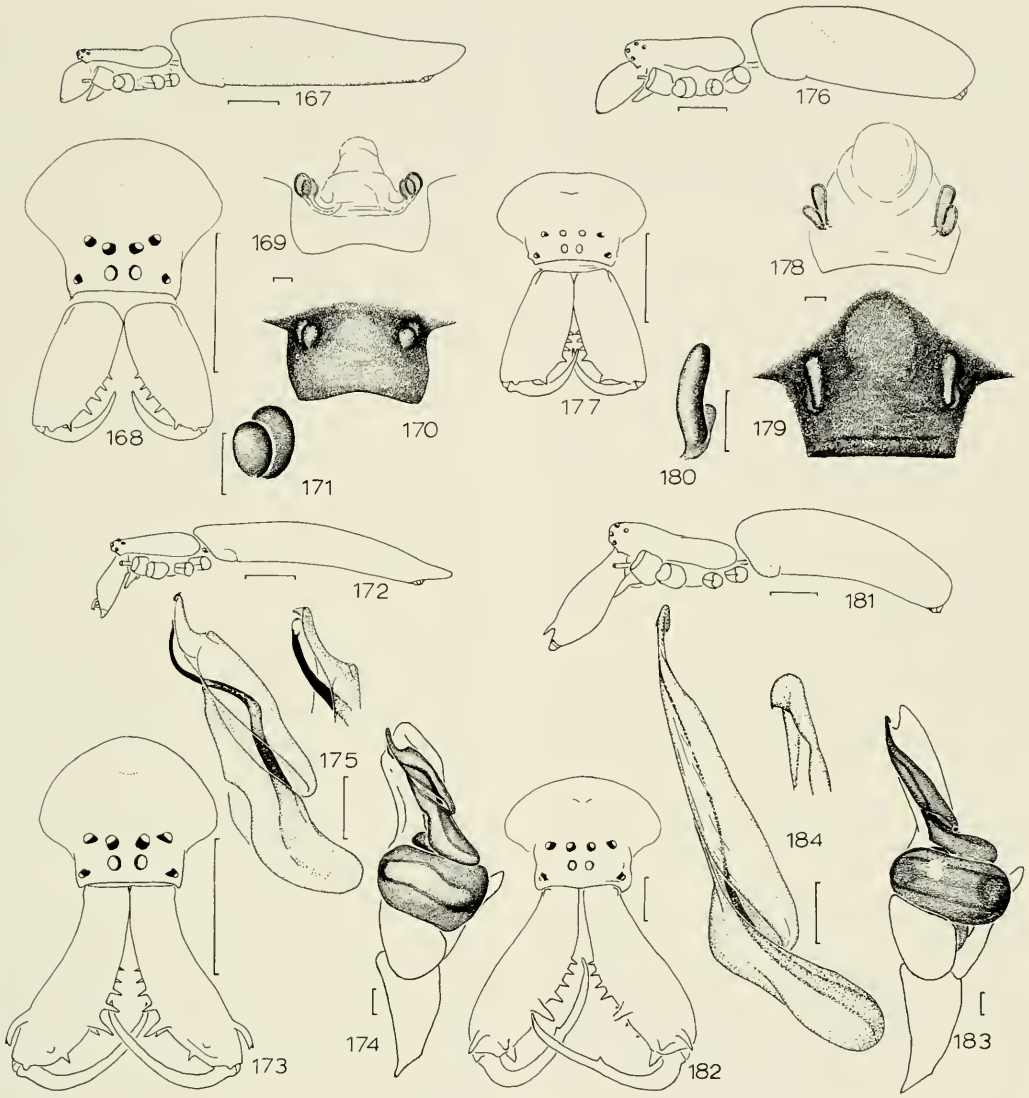
Distribution. From Great Slave Lake, Ontario, Indiana to the Pacific coast (Map 4).

Paratypes. Northwest Territories: 5 mi. S. of Great Slave Lake, 22 July 1944, ♂ (T. Kurata). *Ontario.* Goose Island, Lake Nipissing, 26 July 1931, ♀♀ (T. Kurata). *British Columbia.* Victoria, 1931, ♂. *Indiana.* Steuben Co.: Center Lake, Angola, 23 Aug. 1968, ♀, ♂ (J. Carico). *Illinois.* McHenry Co.: Pistakee Bay, 26 Aug. 1968, ♀, ♂ (J. Carico). *Nebraska.* Scottsbluff Co.: Morrill, on bridge of Glendo Dam overflow, 30 July 1968, ♂ (A. Moreton). *Colorado.* Boulder Co.: Valmont, E. of Boulder, 31 Aug. 1939, ♂ (U. Latham). *Idaho.* Bear Lake Co.: N. shore of Bear Lake, 30 July 1952, ♀♀, ♂♂ (B. Malkin); Mud Lake near Hot Springs, 7 Aug. 1949, ♂♂ (W. J. Gertsch). Twin Falls Co.: Thousand Springs, June 1938, ♀, ♂♂ (W. Ivie). *Utah.* Rich Co.: Laketown, 30 July 1978, ♀♀, ♂ (G. F. Knowlton); Bear Lake, 25 Aug. 1929, ♀, ♂; SE shore Bear Lake, 3 July 1978, ♂ (G. F. Knowlton); Granite, 26 Aug. 1938, ♂ (G. F. Knowlton). Salt Lake Co.: Salt Lake City, 10 July 1947, ♂ (W. Ivie). Sevier Co.: Richfield, July–Aug. 1930, ♂ (W. J. Gertsch). Utah Co.: Utah Lake at mouth of Provo River, 25 June 1941, ♀♀, ♂♂; W. side of Utah Lake, 24 Sept. 1939, ♀♀, ♂♂ (S. Mulaik, W. Ivie). *Washington.* Grant Co.: Dry Falls, Grand Coulee, 4 May 1940, ♀♀, ♂♂ (M. Hatch); 20 June 1954, ♀♀, ♂ (B. Malkin). Pend Oreille Co.: Diamond Lake, 13 Aug. 1934, ♂ (M. Hatch). *California.* Siskiyou Co.: Tule Lake, 15 July 1940, ♀, ♂ (L. W. Saylor).

Tetragnatha branda new species
Plate 7g, h; Figures 167–175; Map 4

Holotype. Male from sweeping salt marsh, Branford Harbor, Connecticut, July 1975 (C. N. Olmstead) in the Museum of Comparative Zoology. The specific name is an arbitrary combination of letters.

Description. Female. Carapace, legs yellow-white. Sternum, labium dusky. There is a median gray longitudinal band on the carapace. Abdomen silvery; sides with some black pigment overlying silver, and venter with a ventral black band. Posterior eyes 0.7 diameters of anterior medians. Anterior laterals 0.5 diameters of anterior medians. Anterior medians are slightly more than their diameter apart, 1.5 from laterals. Posterior median eyes are 3 diameters apart, 2.5 from laterals. The lateral eyes are much farther apart



Figures 167–175. *Tetragnatha branda* n. sp. 167–171. Female. 167. Lateral. 167. Chelicerae and eye region. 169–171. Genital area. 169. Dorsal. 170. Ventral, cleared. 171. Left seminal receptacles, ventral. 172–175. Male. 172. Lateral. 173. Chelicerae and eye region. 174, 175. Left palpus. 174. Ventral. 175. Conductor, embolus, ventral, and tip, mesal.

Figures 176–184. *Tetragnatha vermiformis* Emerton. 176–180. Female. 176. Lateral. 177. Chelicerae and eye region. 178–180. Genital area. 178. Dorsal. 179. Ventral, cleared. 180. Left seminal receptacles, ventral. 181–184. Male. 181. Lateral. 182. Chelicerae and eye region. 183. Palpus, ventral. 184. Conductor with embolus, ventral, and tip, mesal.

Scale lines. 0.1 mm; except Figs. 167, 168, 172, 173, 176, 177, 181, 182, 1.0 mm.

than the medians (Fig. 168). The abdomen is elongate and has a tail overhanging the spinnerets (Fig. 167). Total length, 8.8 mm. Carapace, 2.0 mm long, 1.4 mm wide. First femur, 3.3 mm; patella and tibia, 3.7 mm; metatarsus, 2.7 mm; tarsus, 1.2 mm. Second patella and tibia, 2.7 mm; third, 1.4 mm; fourth, 3.1 mm.

Male. Coloration like female, but with dark pigment. Secondary eyes slightly larger in relation to anterior medians than in female. Anterior median eyes slightly more than their diameter apart, slightly less than two diameters from laterals. Posterior medians slightly more than two diameters apart, the same distance from laterals (Fig. 173). Total length, 6.8 mm. Carapace, 2.2 mm long, 1.3 mm wide. First femur, 3.8 mm; patella and tibia, 4.5 mm; metatarsus, 2.4 mm; tarsus, 1.3 mm. Second patella and tibia, 3.4 mm; third, 1.7 mm; fourth, 3.7 mm.

Variation. Total length of females, 8.8 to 13.8 mm; total length of males, 6.8 to 11.2 mm. All have a relatively short tail.

Diagnosis. The lateral eyes of this species are much farther apart than the medians (Figs. 168, 173). The genitalia (Figs. 169–171) are most like those of *T. vermiformis*, but the species differs by having a tail, the abdomen overhanging the spinnerets.

This species can be confused with *T. caudata*, but the male palpus lacks conductor pleats, and the conductor has a distal, lateral notch (Plate 7g, h; Figs. 174, 175).

The female differs from *T. caudata* by having adjacent, spherical seminal receptacles (Fig. 171).

Natural History. All specimens have been collected from coastal salt marshes.

Distribution. New England to Mississippi (Map 4).

Paratypes. Connecticut. New Haven Co.: Branford Harbor, July 1975, 3♀ (C. N. Olmstead, MCZ). *Georgia.* McIntosh Co.: Sapelo Island, 27 July 1957, ♀ (E. P. Odum, MCZ); July–Aug. 1960, 4♀, 4♂, salt marsh (S. Schmittner, AMNH). *Florida.* Levy Co.: 12 May 1951, ♀, 2♂ (H. K. Wallace, FSCA); Monroe Co.: Cape Sable, 4 June, ♀ (H. V. Weems, FSCA). *Mississippi.* Jackson Co.: Ocean Springs, January 1905, ♀ (J. H. Comstock, CUC).

Tetragnatha vermiformis Emerton
Plate 7i; Figures 176–184; Map 4

Tetragnatha vermiformis Emerton, 1884, Trans. Connecticut Acad. Sci., 6: 333, pl. 39, figs. 12–14, ♀, ♂. One male lectotype and one female paralectotype, plus two female paralectotypes of a different species from Beverly, Massachusetts in the Museum of Comparative Zoology, examined. Seeley, 1928, Bull. New York State Mus., 278: 138, figs. 55–58, ♀, ♂. Roewer, 1942, Katalog der Araneae, 1: 994. Kaston, 1948, Bull. Connecticut Geol. Natur. Hist. Surv., 70: 272, figs. 877–878, ♂. Chickering, 1957, Bull. Mus. Comp. Zool., 116: 349, figs. 103–105, ♂ (not ♀); 1959, Bull. Mus. Comp. Zool., 119: 495, figs. 47–50, ♂ (not ♀).

Eucta vermiformis:—Bonnet, 1956, Bibliographia Araneorum, 2: 1808.

Note. The female specimens illustrated by Chickering had been misidentified.

Variation. Total length of females, 6.7 to 12.3 mm; males, 5.0 to 9.1 mm.

Diagnosis. The lateral eyes are farther apart than the medians, and the abdomen is entirely silver (Figs. 176, 177, 181, 182).

Males can readily be distinguished from the males of the four other species having similar eye placement by the lack of pleats on the long conductor of the palpus. The shape of the conductor tip (Fig. 184) separates *T. vermiformis* from the similar European *T. (Eugnatha) striata*. The absence of a tail distinguishes it from *T. branda* (Plate 7i; Figs. 176, 181, 183, 184).

The female has a much shorter, less worm-shaped abdomen than is seen in the other species with similar eye placement. The abdomen is entirely silver, with fewer spots on the venter. Sometimes there are also black marks on the sides of the abdomen. Unlike *T. caudata*, *T. pallescens*, and *T. straminea*, the seminal receptacles of each pair are narrow

and elongate, placed paraxial, the pair more than twice their length apart and more sclerotized laterally than toward the median (Figs. 178–180).

Natural History. Nothing is known of the habits of this uncommon species. The very similar European *T. striata* is found on reed grass (*Phragmites*) of larger lakes and builds near the open water. It is best collected by using a boat (Wiehle, 1963).

Distribution. Southern Canada, northwest to eastern states to Canal Zone (Map 4).

Records. Ontario. La Seine River, July, ♀ (N. Banks); Lac Seul, Aug. 1919, ♂ (Waugh); Mallorytown Landing, ♀, ♂. *Massachusetts.* Falmouth Co.: Woods Hole, Aug. 1881, ♂ (J. H. Emerton). Nantucket, 9 Sept., ♀, ♂ (J. H. Emerton). *Rhode Island.* Kingston, ♂ (L. G. Worley). *New York,* Long Island: Quogue, Oct. 1948, ♀, ♂ (R. Latham). *Georgia.* Honey Isl. Prairies, Okefenokee Swamp, 31 May 1912, ♀. *Florida.* Alachua Co.: Newnan's Lake, Nov. 1931, ♀, ♂ (T. H. Hubbell). Dade Co.: Tamiami Trail, off Route 27, 19 March 1968 (A. M. Chickering). Lake Co.: Leesburg, March 1954, ♂ (M. Statham). Monroe Co.: Everglades Natl. Park, Shark River area, 1960, ♀. *Michigan.* Walnut Lake, ♂ (A. M. Chickering). Bay Co.: Aug. 1942, ♀ (A. M. Chickering). Calhoun Co.: Albion, July 1930, ♂ (A. M. Chickering). Eaton Co.: Olivet, Sept. 1933, ♂ (A. M. Chickering). Macomb Co.: Selfridge Field, June 1944, ♀, ♂ (B. Malkin). Ogemaw Co.: Aug. 1937, ♂ (A. Peacock). *Indiana.* Steuben Co.: Angola at Center Lake, 25 Aug. 1968, ♂ (J. Carico). *Nebraska.* Holt Co.: Goose Lake, 8 Sept. 1977, ♂ (W. Rapp). *Washington.* Cowlitz Co.: Toutle River, 24 July 1932, ♂ (T. Kincaid).

Panama Canal Zone. Barro Colorado Isl. 6 Feb. 1958, ♀, ♂ (A. M. Chickering).

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A Revision of the Nearctic Beridinae (Diptera: Stratiomyidae)

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A REVISION OF THE NEARCTIC BERIDINAE (DIPTERA: STRATIOMYIDAE)

NORMAN E. WOODLEY[1]

ABSTRACT. The Beridinae (Diptera: Stratiomyidae) from the Nearctic Region are taxonomically revised. Nine species in four genera are recognized. Keys to all taxa, diagnoses for genera and species, and descriptions of each species are presented. Male and female genitalia are illustrated for the first time, and maps of distributions are included.

Beris strobli Dušek and Rozkošný, *Beris fuscipes* Meigen, and *Exodontha dubia* (Zetterstedt) are found to occur in the Nearctic Region, and are thus Holarctic.

The generic name *Exodontha* Rondani is resurrected from synonymy with *Antissa* Walker, and is used for the Holarctic species of the "Antissini." *Hemiberis* Enderlein is removed from synonymy with *Actina* Meigen, and placed in synonymy with *Beris* Latreille.

Beris annulifera var. *luteipes* Johnson is resurrected from synonymy with *Beris annulifera* (Bigot), and raised to specific status. *Beris californica* James, a junior name, is synonymized with *Beris luteipes* Johnson. *Allognosta similis* (Loew) is synonymized with *Allognosta obscuriventris* (Loew). *Beris annulifera* (Bigot) is synonymized with *Beris fuscipes* Meigen. *Exodontha grandis* (James) is synonymized with *Exodontha dubia* (Zetterstedt).

Neotypes are designated for *Beris fuscitarsis* Say and *Sargus dorsalis* Say, the latter a synonym of *Allognosta fuscitarsis* (Say). Lectotypes are designated for *Beris quadridentata* Walker, *Metoponia similis* Loew, and *Oplacantha annulifera* Bigot.

Biological notes are presented for each species based on information in the literature and on specimen labels.

INTRODUCTION

The subfamily Beridinae is a group of primitive Stratiomyidae, as evidenced by their seven undifferentiated abdominal segments, a character shared by the other subfamily considered primitive, the Chiromyzinae. The only species of the latter subfamily in the Nearctic Region is the introduced *Inopus rubriceps* (Macquart), which occurs in the San Francisco Bay area of California. This species is easily recognized by its vestigial mouthparts and its antennal flagellum which lacks distinct annuli. The other subfamilies of Stratiomyidae in North America have an abdomen composed of five principal segments, the sixth and seventh being telescoped within the abdomen. Thus the Beridinae may be easily recognized in the Nearctic Region. The key to genera presented by Cole (1969) will also enable the reader to identify these flies readily at the generic level.

Melander (1904) provided the first synopsis of the Nearactic Beridinae. Curran (1927) improved upon this in his treatment of the Canadian Stratiomyidae, incorporating new species that had been described after Melander's paper. James (1939) again reviewed the subfamily for the Nearctic Region, and his paper established the classification that has been only slightly modified until now. McFadden (1972) synonymized several varieties described by Johnson (1926a, 1926b) with their nominate species, and reduced *Beris canadensis* (Cresson) to synonymy with *Beris annulifera* (Bigot).

Workers on the Palaearctic fauna, notably Rozkošný and his colleagues (Du-

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šek and Rozkošný, 1963; Rozkošný, 1973; Nartshuk and Rozkošný, 1975, 1976) and Nagatomi and Tanaka (1969, 1972), were the first to utilize male genitalia extensively to stabilize species concepts. A number of names were synonymized, and it became easier to compare the Nearctic fauna with the Palaearctic fauna. Subsequently, I examined the genitalia of the Nearctic species of Beridinae for the first time, which has resulted in one synonymy of a Nearctic species with a Palaearctic one, the discovery of two Palaearctic species previously unrecorded from the Nearctic Region, and new synonymies within the Nearctic fauna. In addition, I have examined nearly all types of North American Beridinae (of the types in existence for names used in North America, *Beris fuscipes* Meigen is the only name for which I have not seen a type). This paper reports the results of my study.

Nine species of Beridinae in four genera are now known to occur in North America, three of which are Holarctic. At present it is not possible to discuss evolutionary relationships between the genera that inhabit the Nearctic Region; this must await a worldwide study of generic concepts within the subfamily. The Beridinae are most diverse in southern South America, Australia, and New Zealand, and they remain poorly known in the latter two regions.

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METHODS

Over 4000 specimens have been examined in the course of this work. The genitalia of all known species were examined and illustrated with the aid of an ocular grid in a Leitz binocular dissecting microscope. After being cleared with hot 10% KOH, and neutralized with weak acetic acid followed by a water rinse, the parts were stored in plastic microvials and attached to the pin of the appropriate specimen.

Measurements were made with an ocular micrometer. The frontal width was measured at the anterior ocellus and divided by the width of the head taken at

the same point to arrive at the ratio provided in the description. Lengths of the entire insects were measured from the anterior-most portion of the head to the tip of the abdomen, but do not include the antennae.

Collection data have been summarized, and do not include precise localities for the United States localities except for species that are uncommon or rare. Common species are summarized by county only. Since females of the genus *Exodontha* Rondani are difficult to identify with certainty, the sexes of specimens from each locality are indicated, to give the reader an idea of which localities are best documented.

Stippling indicates internal surfaces of sclerotized structures in all drawings except Figures 48 and 53, where it indicates membrane. In some other figures of the male post-genital segments, areas around the cerci are more or less membraneous, however, though the stippling is meant to indicate the internal surface of the eleventh sternum.

TAXONOMIC CHARACTERS

Most of the taxonomic characters utilized in this study are unambiguous. It seems advisable to comment briefly on the terms used for the male and female genitalia, however, as a variety of terms have been used for the same structures, even within the literature of the Stratiomyidae.

The female genitalia have been found to exhibit useful characters at the specific level, especially the so-called genital furca. This structure evidently represents the highly modified ninth abdominal sternite (Bonhag, 1951), contrary to the statement by Nagatomi and Iwata (1976) that the ninth sternite is absent in most lower Brachycera. In the Beridinae the furca is fused to the ninth tergite. The spermathecal ducts pass through the median aperture of the furca into the genital chamber. In most cases the posterior portions of the ducts are unsclerotized and thus nearly invisible in cleared preparations of the female genitalia. In *Beris fuscipes* Meigen and *B. luteipes* Johnson, however, in which the posterior portions of the ducts are sclerotized, they may be followed all the way to the aperture, which in both species is quite small. The median portions of the ducts are unsclerotized and rather long, leading to the sclerotized anterior portions of the ducts and the spermathecae, which are also sclerotized. The spermathecae are very similar in all species of Beridinae examined, and are three in number. The illustrations of the female genitalia present a ventral view. They are most valuable as specific level characters in *Beris*. Even though they are distinctive for other species, except in the genus *Exodontha*, they are not necessary for routine identification. They are illustrated primarily to assist future workers who may wish to compare Nearctic species with those of other regions.

In describing the male genitalia, I have used the terminology utilized by Hanson (1958) which is evidently derived from that proposed by Michener (1944). Important structures include the gonostylus (=dististylus, telomere), the gonocoxites (=synsternite, basistyle), and the aedeagal complex, which is composed of a median aedeagus (=penis) and lateral aedeagal valves (=penis valves, parameres). The gonocoxites have a rather distinctive shape in each species, with the posterior margin of the ventral bridge being particularly diagnostic. It is often endowed with a median process, which has been called the median process of the synsternite by Rozkošný (1973). Dorsal views are illustrated for both the genital capsule and the aedeagus, as well as a lateral view for the latter structure, which is frequently strongly arcuate. A dorsal view of the post-genital segments is also included, which is composed of the tenth and eleventh tergites and the cerci. The shape of the tenth tergite is often char-

acteristic at the specific level, and in *Beris fuscipes* it possesses posterolateral surstyli.

SUBFAMILY BERIDINAE

Diagnosis. These flies can be separated from other Nearctic Stratiomyidae by the presence of preapical tergal grooves on abdominal tergites two to six in all genera except *Exodontha*. *Exodontha* may be assigned to the subfamily because it possesses a spur on the middle tibia (a character shared with *Allognosta*), which is absent in all other Stratiomyidae outside of the Beridinae. All Nearctic genera except *Allognosta* possess at least four scutellar spines, while taxa outside the Beridinae possess no more than two. Other characters which most members of the subfamily exhibit include porrect antennae, with a simple flagellum normally composed of eight flagellomeres; palpi usually distinct, two-segmented (one-segmented and minute in *Beris*) and porrect; labellae of proboscis not strongly sclerotized; wing venation not as strongly crowded toward anterior margin of wing as in other Stratiomyidae, the wings normally evenly set with microtrichia; M_3 present or absent; M_4 arises from the discal cell; abdomen usually with seven more or less undifferentiated segments (five in *Exodontha*); male genitalia visible externally, aedeagal complex trifid; female cerci two-segmented.

Most North American species of Beridinae are poorly known biologically. The larvae of only two Nearctic species are known and were briefly treated by McFadden (1967). Label data, personal discussions with other entomologists, and morphology suggest that all Nearctic species, with the possible exception of the species of *Exodontha*, form conspecific male swarms. The structure of the male eyes conforms to that reported for swarming Diptera (Downes, 1969; McAlpine and Monroe, 1968), and the inflated hind basitarsus found in males of *Actina* and *Beris* possibly has a function related to swarming behavior. I have personally observed members of the Neotropical beridine genus *Oplachantha* Rondani in male swarms.

KEY TO THE NEARCTIC GENERA OF BERIDINAE

1. Middle tibia with a single, small, apical spur; abdomen ovate 2
   Middle tibia without an apical spur; abdomen elongate 3
2. Scutellum without spines; abdominal tergites with preapical transverse grooves; M_3 absent; smaller species, less than 6 mm. ..... *Allognosta* Osten Sacken (p. 327)
   Scutellum with spines; abdominal tergites without preapical transverse grooves; M_3 present; larger species, greater than 7 mm ..... *Exodontha* Rondani (p. 346)
3. Palpi minute, one-segmented; males holoptic; scutellum normally with six or more spines ..... *Beris* Latreille (p. 336)
   Palpi elongate, two-segmented, easily visible; males dichoptic; scutellum normally with four spines ..... *Actina* Meigen (p. 322)

Genus ACTINA Meigen

Actina Meigen, 1804: 116; type species *Beris nitens* Latreille (Rondani, 1863: 87).

Allactina Curran, 1924: 24; type species *Beris viridis* Say, by original designation.

Diagnosis. Members of the genus *Actina* may be recognized easily by their four scutellar spines and well-developed, two-segmented palpi. It is likely to be confused only with *Beris*, which is also elongate in form, but that genus possesses very minute, one-segmented palpi and at least six scutellar spines. In addition, males of *Actina* are the only Nearctic Beridinae of that sex which are dichoptic. Other generic characters are: eyes pilose in both sexes; antennae with first segment at least two times as long as second, flagellum elongate with eight distinct flagellomeres; face receding, oral margin not produced; palpi slender in male, more robust in female; legs with hind femora much longer than middle and front femora, almost twice as long in males; hind tibiae and femora clavate; hind basitarsi of males noticeably inflated, second hind tarsomere also slightly

inflated; middle tibiae without spurs; wings with R_{2+3} arising at or slightly beyond r-m, R_4 present, M_1 and M_2 petiolate to widely separate at discal cell, M_3 normally absent; abdomen of male parallel-sided, fifth and sixth segments slightly wider, female abdomen slender but ovate; both sexes with tergal grooves on segments two to six; male genitalia with spinose membrane between aedeagal complex and genital capsule; gonostyli with internal median tooth.

There is only one Nearctic species of *Actina*. Elsewhere, there is one European species, several from the eastern Palaearctic, and five species in the Oriental Region (James, 1975). Species from the Australian Region presently ascribed to *Actina* may not be congeneric, but exclusion must await a study of the fauna of that region.

Actina viridis (Say)

Beris viridis Say, 1824: 368.
Actina viridis var. *obscuripes* Johnson, 1926a: 90.

Type Material. The type of *Beris viridis* Say is believed to be destroyed (Lindroth and Freitag, 1969). The material Say examined was from Pennsylvania, and probably consisted of a series of females.

The holotype male of *Actina viridis* var. *obscuripes* Johnson is presently housed in the Museum of Comparative Zoology at Harvard University, Cambridge, Massachusetts (MCZ 27272). The wings are slightly folded, but it is otherwise in excellent condition.

Diagnosis. There is only one species of *Actina* in the Nearctic Region, *A. viridis* (Say), which may be recognized on the basis of the generic characters.

Description. Male. Head black, frons slightly converging toward antennae, 0.19 to 0.22 width of head, shiny green to bluish, silvery pollinose just above antennae, dull velvety black along inner eye margins from level of anterior ocellus to about two-thirds of the way to antennae; face slightly diverging toward oral margin, blackish with slight metallic reflections, grayish pollinose except for very narrow median line; occiput dark pollinose except for cerebrale, which is concolorous with frons; frons (except for small bare area just above pollinose portion), face, upper cerebrale, and outer edge of occiput with long black hairs, each hair slightly bent medially and about the length of the first two antennal segments combined, but pile just above antennae slightly shorter than second antennal segment; genae with darkish pile about two-thirds length of frontal pile; antennae black; first segment 2.5 times as long as second, slender, slightly expanded apically; flagellum about 1.5 times the length of both basal segments combined, conically tapered (Fig. 1); longer hairs of antennae black; eyes with short, dark pilosity; ocellar tubercle slightly prominent; palpi brownish to black, second segment very narrow at base, expanded apically; proboscis yellow, with very pale pile. Thorax shiny metallic green, sometimes ranging to bluish, occasionally with bronzy or coppery reflections, becoming less shiny and more brownish ventrally and just below wing; humeri and postalar calli more blackish brown, the latter sometimes brownish; scutellum with four yellow spines; thoracic pilosity quite variable in color and length: some hairs short and usually mostly pale, longer hairs subequal to frontal hairs or a little longer, ranging from almost wholly pale to mostly dark; pleural pile nearly as long, middle of mesopleuron and hypopleuron bare; legs with coxae brownish, remainder yellowish except for front tarsi, apical three tarsomeres of middle tarsi, apices of hind femora, apical halves of hind tibiae, and apical three tarsomeres of hind tarsi brownish, basal two tarsomeres of hind legs whitish, the extreme apices pale brownish; legs ranging in dark specimens to wholly brownish black except for extreme apices of front and middle femora, extreme bases of all tibi-

ae, extreme bases and ventral surfaces of middle and hind basitarsi as well as ventral surface of second tarsomeres of hind legs, which are yellowish; legs with abundant long pile, pale to dark (always with at least a few dark hairs), on posterior surfaces of front femora; middle femora with a few hairs, shorter than those on front femora, longer ventrally; hind femora with a few longer hairs dorsally at base; posterior surfaces of fore and middle tibiae with a few longer hairs, usually at least two, often six to eight; halter yellow, stem often brownish; wings hyaline, veins brownish, stigma brown and contrasting strongly with wing membrane; the membrane evenly set with microtrichia except at extreme base and basal regions of second basal and anal cells. Abdomen brownish to brownish black, often with metallic reflections on lateral margins of tergites and most of sternites; medial portions of tergites pollinose, sparse on sixth tergite and absent on posterior segments; pile long laterally, subequal to mesonotal pile, somewhat shorter and sparser ventrally; pile of pollinose areas may be dark, pile of other areas pale, but in very dark specimens a few dark hairs may be present on the lateral portion of the first segment; tenth tergite and cerci yellow; genitalia (Figures 11–13, 15) with gonostyli possessing an internal medial tooth; aedeagal complex with lateral valves parallel-sided, slightly widened apically, their inner margins diverging apically (Fig. 12). Length 4.3 to 6.4 mm.

Female. Differs from male as follows: head smaller, with upper frons shinier, almost impunctate, wider (0.25 to 0.31 width of head), and the velvety black spots along eye margins smaller; face with larger central shiny region; pile of head sparser, much shorter (less than the length of the second antennal segment except on genae where it is slightly longer than that segment), and mostly pale, but a few dark hairs sometimes present around antennal bases; antennae longer, with basal two segments yellow, flagellum more slender, basal flagellomere not as wide as in male, the entire flagellum tapering more gradually (Fig. 2); basal flagellomere mostly yellow, inner portions of the next two yellowish, ranging in some specimens to basal three flagellomeres and inner portions of four to six yellowish; hairs on basal segments black; palpi yellow; pile of eyes extremely short and sparse. Thorax with short, pale pile, about the length of that on head but becoming a little longer on pleura; mesonotum bright metallic green to blackish green, humeri and postalar calli yellowish, sometimes brownish; legs wholly yellow except for tarsomeres of front legs and distal three tarsomeres of middle and hind legs brownish, ranging in some specimens to yellow with brownish coloration on apices of hind femora, apical two-thirds of front tibiae, hind tibiae except for short basal regions, front tarsi, apical third of first tarsomere and entire tarsomeres two to five of middle tarsi, apices of basal two tarsomeres and entire tarsomeres three to five of hind tarsi. Abdomen lighter in color, brownish to brownish yellow, often with metallic reflections, especially on basal three tergites, and often with lateral and outer posterior margins of tergites yellowish; sternites ranging from wholly brownish to wholly yellow, without metallic reflections; cerci yellow; pile of abdomen shorter than in male, wholly pale; genitalia (Fig. 14) with posterolateral processes of furca long, converging; posterior portions of spermathecal ducts unsclerotized; median aperture of furca large. Length 4.2 to 5.9 mm.

Distribution (Map 1). Nearctic; northern British Columbia east to Labrador. south to Utah, New Mexico, east to northern Georgia.

Locality Records (1149 males; 703 females). CANADA: *Alberta:* Cooking Lake; Edmonton; Gull Lake; Jumping Pond Creek, 20 mi. W of Calgary; Slave

Lake; Wabamun. *British Columbia:* Fort Nelson; Gagnon Rd., 6 mi. W of Terrace, 220 ft.; Terrace; Trinity Valley; Vernon. *Labrador:* Goose Bay. *Manitoba:* Aweme; Carberry; Cedar Lake; Minnedosa; Ninette; 5 mi W. of Shilo; Treesbank. *New Brunswick:* Hwy. 27, 8 mi. S of McAdams; Barber D.; E. Sussex; Penobsquis Camp, Rte. 1; St. Jacques; St. John. *Newfoundland:* Mts. E of Codroy; Lomond. *Nova Scotia:* Truro. *Ontario:* Bell's Corners; Black Rapids; Brittania; Coldwater; Crozier; 6 mi. S of Devlin; Dryden; Eagle; Finland; Ft. Frances; Go Home Bay, 8 mi. W of Bala; Grimsby; Guelph; Hallville; Jordan; Kingsville; Low Bush, Lake Abitibi; Marmora; Maynooth; Mer Bleu; Moose Factory; Normandale; Ogoki; Orillia; Osgoode; Ottawa; Petawawa; Pinewood; Pt. Pelee; Port Hope; Rainy River; Rondeau; Simcoe; Stittsville; Sturgeon Bay; Tillsonburg; Tobermory. *Quebec:* Abbotsford; Anticosti; Aylmer; Beechgrove; Breckenridge; Burbridge; Fabre; Fairy Lake; Farnham; Gaspe; Gracefield; Harrington Lake, Gatineau Park; Hull; Kazubazua; Knowlton; Laniel; La Verendrye Prov. Park, Rte. 58, mi. 139; Megantic; Mistassini Post; Montreal; Mt. Orford, 1200 ft.; Mt. Ste. Hilaire, 500–700 ft.; Nominingue; Old Chelsea, King Mt., 1500 ft.; Queens Park; Roundtop Mt., 1300 ft., Sutton; Rupert House; Ste. Anne des Monts; Valtetreau. *Saskatchewan:* Big River; Glaslyn; Kenosee. UNITED STATES: *Arkansas:* Garland Co.; Mississippi Co.; Washington Co. *District of Columbia:* Washington. *Georgia:* Clarke Co.; Dawson Co.; DeKalb Co.; Houston Co.; Lumpkin Co.; Rabun Co.; Towns Co.; Union Co. *Illinois:* Adams Co.; Boone Co.; Champaign Co.; DeWitt Co.; Douglas Co.; DuPage Co.; Jackson Co.; Lake Co.; LaSalle Co.; McHenry Co.; McLean Co.; Macoupin Co.; Mason Co.; Morgan Co.; Rock Island Co.; Tasewell Co.; Union Co.; Vermilion Co. *Indiana:* Marion Co.; Pulaski Co.; Tippecanoe Co. *Iowa:* Boone Co.; Story Co.; Woodbury Co. *Kansas:* Douglas Co.; Johnson Co.; Leavenworth Co.; Lyon Co.; Riley Co. *Kentucky:* Greenup Co.; Nelson Co. *Maine:* Hancock Co.; Piscataquis Co. *Maryland:* Montgomery Co.; Prince Georgés Co. *Massachusetts:* Berkshire Co.; Essex Co.; Middlesex Co.; Norfolk Co.; Worcester Co. *Michigan:* Arenac Co.; Charlevoix Co.; Chippewa Co.; Delta Co.; Hillsdale Co.; Ingham Co.; Kalamazoo Co.; LaPeer Co.; Livingston Co.; Roscommon Co.; Washtenaw Co.; Wayne Co. *Minnesota:* Anoka Co.; Carver Co.; Clay Co.; Clearwater Co.; Cook Co.; Crow Wing Co.; Dakota Co.; Fillmore Co.; Freeborn Co.; Goodhue Co.; Hennepin Co.; Houston Co.; Koochiching Co.; Lake Co.; Lake of the Woods Co.; Lyon Co.; Marshall Co.; Mille Lacs Co.; Norman Co.; Olmstead Co.; Pine Co.; Pipestone Co.; Pope Co.; Ramsey Co.; Red Lake Co.; Rice Co.; Roseau Co.; St. Louis Co.; Wabasha Co.; Wadena Co.; Washington Co.; Winona Co. *Mississippi:* Lafayette Co. *Missouri:* Jackson Co.; Phelps Co. *Nebraska:* Boone Co.; Cass Co.; Cherry Co.; Lancaster Co.; Sharpy Co. *New Hampshire:* Grafton Co. *New Jersey:* Bergen Co.; Burlington Co.; Gloucester Co.; Ocean Co.; Sussex Co. *New Mexico:* Otero Co. *New York:* Clinton Co.; Cortland Co.; Erie Co.; Lewis Co.; Niagara Co.; Ontario Co.; Orange Co.; Oswego Co.; Suffolk Co.; Tompkins Co. *North Carolina:* Buncombe Co.; Graham Co.; Haywood Co.; Jackson Co.; Johnston Co.; Macon Co.; Pender Co.; Swain Co.; Yancey Co. *Ohio:* Delaware Co.; Franklin Co.; Hocking Co.; Madison Co.; Ottawa Co.; Summit Co.; Tuscarawas Co. *Pennsylvania:* Dauphin Co.; Erie Co.; Indiana Co.; Lebanon Co. *Rhode Island:* Washington Co. *South Dakota:* Grant Co. *Tennessee:* Campbell Co.; Hamilton Co.; Knox Co.; Montgomery Co.; Sevier Co. *Texas:* Dallas Co. *Utah:* Millard Co. *Vermont:* Bennington Co.; Caledonia Co.; Orleans Co.; Windham Co. *Virginia:* Arlington Co.; Augusta Co.; Fauquier Co.; Fairfax Co.; Page

Co.; Roanoke Co. *West Virginia:* Hampshire Co.; Jefferson Co. *Wisconsin:* Dane Co.; Door Co.; Polk Co.; Sauk Co.; Washburn Co.

Flight Period. Specimens have been collected from 25 March (only two March records) to 30 July. The predominant months of activity are May and June throughout the range, although in southern states a number of specimens have been collected in April.

Biology. The larval stages of *Actina viridis* are unknown, but the larva of *Actina nitens* (Latreille), a closely related European species, is being described by Rozkošný (in preparation). Adults have been taken at black lights and in Malaise traps. They have also been collected on a number of plants, presumably by sweeping: alfalfa (Minnesota, New York), aspen (Alberta), *Barbarea* (Ontario), cedar (Quebec), choke cherry (Manitoba), *Equisetum* (Manitoba), *Geranium maculatum* (Virginia), *Ledum* (Ontario), locust (Georgia), Norway pine (Minnesota), *Prunus virginiensis* (Illinois), *Prunus* sp. (Nebraska), *Ribes* sp. (Manitoba), *Salix* sp. (Alberta, Ontario, Nebraska), and *Taraxacum officinale* (Ontario). Males have been collected in conspecific swarms in wooded areas in Kansas (McGinley, personal communication).

Remarks. Actina viridis is the most common member of the subfamily in North America, and is one of the most common Stratiomyidae in the Nearctic Region. It cannot easily be confused with any other species. Since the lectotype designation presented elsewhere in this paper has removed *Beris quadridentata* Walker from synonymy with this name, there are no synonymous specific names, only one varietal one. Consequently, there seems to be no reason for designating a neotype for this species at present, even though the original type material is destroyed. Any such action should be left to future authors, if additional species of the genus are discovered in the Nearctic Region. Say's mention in the original description of the bright green coloration of the head and thorax and the four yellowish scutellar spines leaves little doubt that he was describing this common species.

This species is quite variable. Color, particularly of the legs, varies greatly. The legs range from largely yellow to almost wholly blackish brown. Darker specimens are found in the northern areas of the range, and at high altitudes in more southern areas. In fact, the darkest specimens I have examined were from Clingman's Dome, Great Smoky Mountains National Park, Tennessee. There is also a gradual trend toward smaller size toward more northern latitudes. It seems likely that the darker specimens are a result of environmental conditions, perhaps cold temperatures. Johnson's *Actina viridis* var. *obscuripes* is based on dark specimens from Anticosti, Quebec, and the name was synonymized by McFadden (1972). I agree with his decision as there is no sharp difference between any light and dark forms with respect to geographic location such that a subspecific designation is warranted. Wing venation in the species is also variable. The bases of M_1 and M_2 at the discal cell may be petiolate, or widely separate, or anywhere between these two extremes. I have observed specimens collected at the same locality on the same day with the entire range of variation. M_3 is occasionally present in some specimens as a small stub, sometimes only on one wing. One otherwise typical specimens was noted with R_4 absent.

Because of the variable nature of this species, I checked genitalia from a number of localities as well as from light and dark forms to try to detect any differences that might indicate more than one species was present. Although the shape of the gonostyli is somewhat variable, particularly with respect to the size of the lobe above the median tooth, I detected no differences that indicated the presence of more than one species. The shape

of the lateral valves of the aedeagal complex is particularly diagnostic, and is quite constant. I have examined the aedeagal complex of *Actina nitens* as well as a species from Taiwan for comparison, and both were distinctly different from *Actina viridis*. Thus, at present, it can be concluded that one rather variable species of *Actina* occurs in the Nearctic Region.

Genus ALLOGNOSTA Osten Sacken

Allognosta Osten Sacken, 1883: 297; type species *Beris fuscitarsis* Say (Coquillett, 1910: 505).

Diagnosis. Members of the genus *Allognosta* may be separated from other Beridinae in North America by the lack of spines on the scutellar margin. All other genera in the Nearctic Region have at least four scutellar spines. Other features exhibited by the genus include: eyes bare to sparsely pilose; males holoptic, females dichoptic; antennae with simple, eight-segmented flagellum; palpi large, two-segmented; middle tibiae with one small apical spur; abdomen flattened, ovate, the seventh segment somewhat reduced; tergites two to six with preapical grooves; wing with R_4 and r-m present, M_3 absent, M_1 and M_2 separate at discal cell.

Enderlein (1921), apparently unaware of Coquillett's designation of *Beris fuscitarsis* Say as the type species for *Allognosta*, designated the Palaearctic species *Metoponia vagans* Loew as the type species. This is, of course, invalid, as Coquillett's designation was earlier.

There are three valid species of *Allognosta* in North America, found primarily in the eastern half of the continent. Although there are no synonyms of the generic name, only *A. brevicornis* was described in the genus. Early authors described species in *Beris* or *Sargus*, and two others were described in *Metoponia*. This last name is based upon a type species in the Chiromyzinae, and it is not surprising that members of *Allognosta* were described in that genus since the Chiromyzinae also have the sixth and seventh abdominal segments rather large and undifferentiated, and lack scutellar spines.

Allognosta occurs in the eastern Palaearctic Region, and is particularly rich in species in the Oriental Region, where there are currently 25 nominal species (James, 1975). Species from Africa presently placed in *Allognosta* may belong in other genera, but I have not examined any specimens of the two species described from that continent.

KEY TO THE NEARCTIC SPECIES OF *ALLOGNOSTA*

1. Males (holoptic) 2
   Females (dichoptic) 4
2. Hairs of face silvery, at most as long as first antennal segment; ventral portion of mesopleuron usually with shiny area devoid of pollinosity; medial portion of ventral bridge of gonocoxites weakly produced, with only two small lobes (Fig. 23) ..... *fuscitarsis* (Say)
   Hairs of face usually dark, and usually longer than the first antennal segment; ventral portion of mesopleuron without bare, shiny area; medial portion of ventral bridge of gonocoxites strongly produced (Figs. 19, 28) 3
3. Antennae short, the flagellum strongly tapering toward apex (Fig. 3); mesonotum somewhat shiny, usually bronzy black; process of ventral bridge of gonocoxites strongly bilobed (Fig. 19); gonostylus rounded at apex ..... *brevicornis* Johnson
   Antennae longer, the flagellum more slender and tapering more gradually toward apex (Fig. 5); mesonotum less shiny due to coarser punctation, although it may have metallic reflections; process of ventral bridge of gonocoxites only feebly emarginate at middle (Fig. 28); gonostylus pointed at apex ..... *obscuriventris* (Loew)
4. P[illegible] reddish to yellowish; frons below transverse sulcus wholly pollinose ..... *brevicornis* Johnson
   Pleura dark, nearly concolorous with mesonotum; frons below transverse sulcus normally with lateral bare areas 5
5. Mesopleuron with a ventral, shiny, bare area; face with hairs pale, no longer than the first antennal segment; disc of abdomen often yellowish, contrasting with lateral margins ..... *fuscitarsis* (Say)
   Mesopleuron without a ventral, shiny, bare area, completely pollinose; face with

hairs usually blackish, longer than first antennal segment; disc of abdomen usually dark ..... *obscuriventris* (Loew)

Allognosta brevicornis Johnson

Allognosta brevicornis Johnson, 1923: 71.

Type Material. The holotype specimen is presently housed in the Museum of Comparative Zoology (MCZ 14928). It is a male from Norwich, Vermont. It is missing the right flagellum of the antennae, the right middle leg, and both hind legs; the right wing and abdomen are glued to a small paper card attached to the pin below the specimen.

Diagnosis. Females are distinguished easily from other Nearctic species of the genus by the reddish and yellowish pleura. Males may be recognized by their short antennae and distinctive genitalia, especially the strongly bilobed medial process of the ventral bridge of the gonocoxites (Fig. 19). The small size is somewhat distinctive, as is the wholly dark abdomen.

Description. Male. Head brownish to black, frons and face densely silvery gray pollinose, rest of head grayish pollinose except for genal area, cerebrale, and the somewhat prominent ocellar tubercle, which are shiny; pile of face brownish, a little longer than the first antennal segment, that on genae longer than the first two antennal segments combined, pale to blackish; antennae about 0.7 times length of head, first two segments brownish to black, second sometimes yellowish; flagellum brownish black, sometimes with first flagellomere and inner portions of flagellomeres two to five yellowish; longer hairs of antennae black; palpi with first segment yellowish to brownish, second dark brown, both with dark hairs, first segment with a few pale hairs; proboscis yellowish. Thorax with mesonotum and scutellum dark brownish black with faint bronzy reflections, humeri and postalar calli paler; pleura brownish, sclerites directly beneath wing more yellowish; prothorax and pleura pollinose except for most of sternopleuron and pteropleuron; mesonotal pile mostly dark, pleural pile with a mixture of pale and dark hairs; legs with front and middle coxae yellowish, hind coxae brownish yellow, femora yellow except for apices of hind femora evanescently brownish; tibiae yellowish, grading evenly to brownish on apical halves, tarsi brown except for extreme apices of tarsomeres one to four of all tarsi, and basal three-fourths of hind basitarsi, yellowish; halter brown, stem yellowish; wing light brownish, evenly set with microtrichia, stigma weakly contrasting with rest of wing. Abdomen brown, dorsally thinly pollinose; longer hairs mostly dark dorsally, mostly pale ventrally; hypopygium concolorous with abdomen; genitalia (Figs. 16–19) with gonostyli large, scoop-shaped, the inner apical surface strongly concave (Fig. 19); medial process of ventral bridge of gonocoxites strongly produced, bilobed, apices of lobes with short spicules (Fig. 19); aedeagus shorter than lateral valves, which diverge slightly at apex (Fig. 17). Length 4.2 to 4.4 mm.

Female. Differs from male as follows: head brownish to blackish, gray pollinose on frons below transverse sulcus and face, faintly so on dorsolateral border of occiput, rest of head shiny, finely punctate; pile of head pale, shorter than first antennal segment except on genae, where it is a little longer than that segment; frons gradually narrowing toward antennae, 0.40 to 0.50 width of head at anterior ocellus; first two antennal segments yellow, flagellum usually with inner portions of flagellomeres two to five extensively yellowish; palpi with first segment usually yellowish. Thorax with entire prothorax, humeri, postalar calli, and pleura of mesothorax yellowish, except for basal three-fourths of sternopleuron which is brownish, although the mesopleuron occasionally has evanescent brownish tinges; mesonotal pile pale, more appressed and shorter than in male, rest of thoracic pile also pale; legs with

coxae, femora, and tibiae yellow, sometimes with tibiae brownish as in male; tarsi with basal halves of all front and middle tarsomeres often yellowish, otherwise as in male; halter with knob yellow to brown; genitalia (Fig. 32) with furca reduced, the median aperture very large; lateral processes present and strongly diverging anteriorly; spermathecal ducts unsclerotized posteriorly. Length 3.9 to 4.9 mm.

Distribution (Map 2). Quebec and New Brunswick south to Tennessee and North Carolina, and west to British Columbia.

Locality Records (6 males, 41 females). CANADA: *Alberta:* Elk Island. *British Columbia:* Kleanza Creek, 14 mi. E of Terrace; Lac la Hache. *New Brunswick:* Doaktown, Hwy. 8. *Ontario:* Maynooth; One Sided Lake; Ottawa. *Quebec:* Bolton Pass, Knowlton, 800 ft.; Duncan Lake, near Rupert; King Mtn., Old Chelsea. UNITED STATES: *Maine:* Salisbury Cove; Hancock Co., Bar Harbor; Penobscot Co., Passadumkeag. *Massachusetts:* Essex Co., Gloucester. *Minnesota:* Itasca Co., T-57, R-24, S-26. *New Hampshire:* Cheshire Co., Jaffrey. *New York:* Uphill Brook, 3200 ft.; Essex Co., Lake Tear, 4300–4600 ft.; Greene Co., 2500 ft. *North Carolina:* Highlands, 3800 ft.; Graham Co., Robbinsville. *Tennessee:* Monroe Co., 20 mi. E of Tellico Plains, 2080 ft. *Vermont:* Bolton Mtn.; E. Charleston; Windsor Co., Norwich.

Flight Period. Collection dates range from 26 May to 9 August, with most specimens being taken in June or July.

Biology. The immature stages are unknown. Adults have been collected on "liliaceous undergrowth-hemlock forest" (British Columbia), "ex *Spiraea*" (Ontario), and by sweeping *Kalmia angustifolia* (Quebec).

Remarks. Allognosta brevicornis remains the least known species of the genus in North America. Specimens, particularly of males, are rare in collections. Consequently, little can be said concerning the range of variation within the species, but it is easily recognizable. It is the only member of the genus known to occur west of the Rocky Mountains.

Allognosta fuscitarsis (Say)

Beris fuscitarsis Say, 1823: 29.
Sargus dorsalis Say, 1824: 377.
Sargus pallipes Wiedemann, 1830: 41.
Beris brevis Walker, 1848: 127.
Beris lata Walker, 1848: 127.

Type Material. The type (sex not stated, and not determinable from the original description) of *Beris fuscitarsis* Say was described from Pennsylvania. The scutellum was broken; thus Say could not have known that it was spineless, and thus he placed the species in *Beris*. The specimen is believed to be destroyed (Lindroth and Freitag, 1969), and to preserve the stability of the present usage of this name, it seems advisable to designate a neotype. I hereby designate a male specimen in the Museum of Comparative Zoology as neotype of this species; it is labeled "Lehigh Gap VII.9.07 Pa/ Collected by C. T. Greene/ Collection C. W. Johnson/ NEOTYPE Beris fuscitarsis Say, 1823: 29 des. N. E. Woodley 1980 MCZ # 32553/ Allognosta fuscitarsis (Say) det. Woodley 1979." The neotype label is red. The specimen fits the original description fairly well. Although the description is brief, the pale disc of the abdomen with "brown incisures" and coloration of the legs of the neotype specimen agree with it. The neotype is from Pennsylvania and agrees with my diagnosis of this species, which is given below. The neotype is missing the right front leg, but is otherwise in good condition.

The type material of *Sargus dorsalis* Say is also lost. It seems quite likely that it was conspecific with *A. fuscitarsis* as suggested by previous authors. Say's description of the abdomen and legs especially seems to fit *A. fuscitarsis*, but could be interpreted as fitting light-colored specimens of *A. obscuriventris* (Loew). The latter interpretation, if fol-

lowed, would cause *Sargus dorsalis* to have priority over *Metoponia obscuriventris* Loew, a name that has seen long standing use. To preserve the present synonymy, it seems best to designate a neotype for *Sargus dorsalis*. I am hereby designating a male specimen in the Museum of Comparative Zoology as neotype, labeled: "Lexington, Ky. May 19–24, 1972 Malaise Trap/ P. H. Freytag Collector/ NEOTYPE Sargus dorsalis Say, 1824: 377 des. N. E. Woodley 1980 MCZ # 32554/ Allognosta fuscitarsis (Say) det. Woodley 1979." The specimen fits the Say description quite well, except that the fourth and fifth abdominal tergites are pale yellow on the disc. Say, in mentioning that the first three tergites were pale centrally, probably was referring to the first four, as the first and second tergites are fused and the suture is obsolete. The neotype is from Kentucky, which was cited as the type locality by Say. He mistakenly placed the species in *Sargus*, probably because the scutellum lacked spines and the third antennal segments were broken off. Say stated that he examined both male and female specimens, but mentioned that the sexes were similar. He probably saw only males, as females of this species have widely separated eyes, which he probably would have noted. Males are indicated by his statement "stemmata approximate on vertex." The neotype male fits my diagnosis of *A. fuscitarsis* presented below.

The name *Sargus pallipes* Wiedemann remains somewhat enigmatic. Wiedemann attributed the name to Say, although the latter described only one Nearctic Stratiomyidae with the name *pallipes*, and that clearly belongs to the genus *Nemotelus* Geoffroy. It is curious that the names *Beris fuscitarsis* and *Nemotelus pallipes* appear on the same page of Say's work (1823: 29), and that the type locality of both is cited as "Pennsylvania," the same locality given by Wiedemann for *Sargus pallipes*. It seems at least possible that Wiedemann made some sort of transcription error, and was really referring to *A. fuscitarsis*, but it seems unlikely in that case for him to have attributed the name to *Sargus*, since he had earlier combined Say's *Sargus dorsalis* with *Beris* (Wiedemann, 1828: 540). If, however, Wiedemann was describing a specimen that he thought was a new species, it was probably in Say's collection and is now destroyed, as he mentioned that it was in the Philadelphia museum. Due to the uncertainty surrounding the name, I prefer not to designate a neotype for it, particularly since Wiedemann attributed the name to Say. It may well be a *nomen nudum*.

The types of *Beris brevis* and *Beris lata*, both described by Walker (1848), are in the British Museum. I have examined both specimens, and they are clearly *Allognosta fuscitarsis*, as has been noted previously by various authors. I have added determination labels to both. The specimen of *Beris brevis* was not previously labeled as a type, but has a locality label stating "Trenton" and another label reading "New York, pres. by E. Doubleday." These agree with the information published by Walker with his description. I have added a red label indicating that this is the type, and the fact that I added the label.

Diagnosis. Males and females may be separated from other species of Nearctic *Allognosta* by the unique shiny, bare area on the ventral portion of the mesopleuron. The male genitalia are diagnostic, particularly the posteromedian portion of the ventral bridge of the gonocoxites, which is not produced as in the other two species (Fig. 23); this is usually visible without dissection. Other diagnostic features include the long basal flagellomere of the antenna (Fig. 4), and the short, pale facial hairs. The transparent wing with contrasting stigmal area is also characteristic.

Description. Male. Head black, frons and face densely silvery pollinose except for a tiny, shiny triangle dorsally on frons;

ocellar tubercle shiny black, somewhat prominent; rest of head grayish pollinose, becoming less dense on genal region and on cerebrale; face with pale pile about the length of the first antennal segment, genal region with pale pile somewhat longer than the first two antennal segments combined; eyes bare; antennae (Fig. 4) about 0.8 times length of head, with first two segments and first two flagellomeres yellow (first segment sometimes brownish), apical flagellomeres brownish black, sometimes yellowish on inner portions of three to five; longer hairs of antennae black; palpi brownish black, with a mixture of pale and dark hairs; proboscis yellowish. Thorax with mesonotum and scutellum shiny black, humeri and postalar calli usually paler, brownish to yellowish; prothorax and pleura brownish black, with thin silvery pollinosity except for shiny, bare areas on extreme dorsal, ventral, and posterior margins of mesopleuron, a large posteromedial patch and ventral portion of sternopleuron, and most of pteropleuron; longer hairs of thorax pale; legs yellow except for dark brownish coloration on apical two-thirds of fore tibiae (especially dorsally), fore tarsi, apical four tarsomeres of middle tarsi, hind tibiae except extreme bases, apical three tarsomeres of hind tarsi, and rather diffuse anterior areas on the hind femora (rarely entire hind femora dark); ranging in some specimens to light brown, with yellow areas on fore tibiae and hind femora reduced; hind coxae brownish; wings almost clear, evenly set with microtrichia, with evanescent infuscation anteriorly; stigma dark, contrasting strongly with the rest of wing; halter with stem yellow, knob yellow with brownish base to wholly brown. Abdomen creamy yellow except for lateral margins and narrow posterior margins of tergites one to four, lateral margin and apical half of tergite five, and remaining tergites dark brown, often with tergite five wholly brown; sternites one to four with lateral margins evanescently brownish, remaining sternites brownish; pile of abdomen mostly dark dorsally, pale ventrally; hypopygium brownish, becoming yellow on gonostyli and cerci; genitalia (Figs. 20–23) with medial region of ventral bridge of gonocoxites not produced, feebly bilobed (Fig. 23); gonostyli arcuate, slender, rounded apically; aedeagus slightly shorter than lateral valves, which diverge slightly apically, the three lobes of the complex well separated (Figs. 21, 22). Length 4.3 to 6.1 mm.

Female. Differs from male as follows: head brownish black, silvery gray pollinose below transverse sulcus of frons except areas on each side slightly above and lateral to antennae, which are nearly bare and shiny; upper frons subparallel to slightly convergent toward antennae, 0.33 to 0.41 width of head at anterior ocellus, diverging below transverse sulcus, finely punctate, middle with elongate, oval, shallow depression; antennal flagellomeres three to five usually yellowish internally, rest brownish to black. Thorax with thin dorsal strip and entire ventral half of mesopleuron bare and shiny. Abdomen ranging in coloration from that described for male to wholly dark brown, usually with pale markings when present restricted to medial portions of tergites; tenth tergite and cerci yellowish; genitalia (Fig. 31) with furca emarginate laterally, the median aperture truncate anteriorly; spermathecal ducts unsclerotized posteriorly. Length 4.1 to 6.3 mm.

Distribution (Map 4). Nova Scotia and northern Maine west to southern Manitoba, south to Arkansas and northern Florida.

Locality Records (383 males; 577 females). CANADA: *Manitoba:* 5 mi. W of Shilo. *New Brunswick:* Fredericton. *Nova Scotia:* Lockeport; Truro. *Ontario:* Anacaster; Blackburn; Cornwall; Emo; Finland; Fort Frances; Grimsby; Jordan; Kelly Lake; Mer Bleu, 5 mi. E of Ottawa; Niagara Falls; Orillia; Ottawa; Picton; Pt. Pelee; Simcoe; Smith's Bay, near Picton;

Stittsville. *Quebec:* Belanger; Breckenridge; Fabre; Hemmingford; Knowlton; Laval; Missisavoir River, Bolton; Montreal; Richelieu; Wakefield. UNITED STATES: *Alabama:* Lee Co. *Arkansas:* Conway Co.; Mississippi Co. *Connecticut:* Fairfield Co.; Hartford Co.; Litchfield Co.; New Haven Co. *District of Columbia:* Washington. *Florida:* Alachua Co. *Georgia:* Clarke Co.; Floyd Co.; Fulton Co.; Oconee Co.; Rabun Co.; White Co. *Illinois:* Adams Co.; Bond Co.; Bureau Co.; Carroll Co.; Champaign Co.; Jo Daviess Co.; Kane Co.; Lake Co.; La Salle Co.; McHenry Co.; McLean Co.; Macoupin Co.; Madison Co.; Ogle Co.; Tazewell Co.; Union Co.; Vermilion Co.; Winnebago Co. *Indiana:* Brown Co.; Marion Co.; Randolph Co.; Tippecanoe Co. *Iowa:* Johnson Co.; Scott Co.; Story Co.; Woodbury Co. *Kansas:* Douglas Co. *Kentucky:* Bullitt Co.; Fayette Co.; Nelson Co. *Maine:* Aroostook Co.; Hancock Co.; Oxford Co.; Penobscot Co.; York Co. *Maryland:* Anne Arundel Co.; Montgomery Co.; Prince Georgés Co. *Massachusetts:* Barnstable Co.; Berkshire Co.; Essex Co.; Hampden Co.; Hampshire Co.; Middlesex Co.; Suffolk Co.; Worcester Co. *Michigan:* Berrien Co.; Cheboygan Co.; Clinton Co.; Ingham Co.; Livingston Co.; Wayne Co. *Minnesota:* Aitkin Co.; Clay Co.; Dakota Co.; Dodge Co.; Fillmore Co.; Goodhue Co.; Hennepin Co.; Houston Co.; Itasca Co.; Lac Qui Parle Co.; Lyon Co.; Olmstead Co.; Pine Co.; Pipestone Co.; Polk Co.; Ramsey Co.; Roseau Co.; Winona Co. *Mississippi:* Lafayette Co. *Missouri:* Boone Co.; Wayne Co. *Nebraska:* Antelope Co.; Cuming Co. *New Hampshire:* Grafton Co.; Sullivan Co. *New Jersey:* Bergen Co.; Burlington Co.; Essex Co.; Hunterdon Co.; Somerset Co. *New York:* Broome Co.; Cayuga Co.; Clinton Co.; Herkimer Co.; Jefferson Co.; Lewis Co.; Madison Co.; Monroe Co.; Nassau Co.; Ontario Co.; Otsego Co.; Seneca Co.; Steuben Co.; Sullivan Co.; Tioga Co.; Tompkins Co.; Westchester Co.; Wyoming Co. *North Carolina:* Buncombe Co.; Graham Co.; Haywood Co.; Macon Co.; Mitchell Co.; Wake Co.; Watauga Co. *North Dakota:* Cass Co. *Ohio:* Champaign Co.; Erie Co.; Franklin Co.; Greene Co.; Hocking Co.; Lawrence Co.; Logan Co.; Medina Co.; Pickaway Co.; Seneca Co.; Summit Co.; Wayne Co. *Pennsylvania:* Allegheny Co.; Bedford Co.; Bucks Co.; Centre Co.; Dauphin Co.; Delaware Co.; Huntingdon Co.; Philadelphia Co.; Westmoreland Co. *Rhode Island:* Richmond. *South Dakota:* Grant Co. *Tennessee:* Anderson Co.; Union Co. *Vermont:* Orleans Co.; Rutland Co.; Windham Co.; Windsor Co. *Virginia:* Fairfax Co.; Giles Co.; Montgomery Co.; Prince George Co.; Shenandoah Co. *West Virginia:* Preston Co. *Wisconsin:* Dane Co.; Polk Co.; Rusk Co.

Flight Period. Collection dates range from 20 April to 1 September. Most specimens have been collected in June and July, with a fair number in August and May. This species seems to have a fairly long flight period even in one region, since I have seen almost the entire range of collection dates from specimens collected at a single locality.

Biology. The larvae of *Allognosta fuscitarsis* evidently live in decaying organic matter (McFadden, 1967). During a study of reclaimed strip mine areas in Ohio, large numbers of larvae were collected in Berlese samples (Triplehorn, personal communication). The record of *A. fuscitarsis* larvae from stems of aquatic plants (McFadden, 1972) seems unusual. One adult specimen from Maryland was annotated "reared-horse manure." Adults have been taken at light, by sweeping, and in Malaise traps. They have been taken from quite a few different plants; labels indicate collections from: alfalfa (New York, Georgia), *Barbarea vulgaris* (Massachusetts), bluegrass (Minnesota), *Catalpa* leaves (North Carolina), elm (New Jersey), *Eupatorium maculatum* (New York), and vetch (Tennessee). The record of *A. fuscitarsis*

taken on *Kalmia* (McFadden, 1972) is erroneous; the specimen referred to was actually *Allognosta brevicornis*. Male specimens from New York were examined that had a label that indicated they were collected from conspecific swarms. It seems probable that all members of the genus have this behavior.

Remarks. Allognosta fuscitarsis is the most common member of the genus in North America, and is present in most collections. Malaise traps have turned up rather long series in a single day, also attesting to the commonness of the species.

The species has previously been characterized by the pale color of the middle portions of the abdominal tergites. This has been found to be quite variable in females, which has led to some previous misidentifications. I have seen series collected on the same day from the same locality which exhibit a range of variation from totally dark brown to rather extensively pale. The species is much more easily identified reliably by the shape of the antennae, the bare area on the mesopleuron, and the genitalia of both sexes. Males are less variable, and I have not seen specimens with totally brown abdomens. However, I have seen specimens of *A. obscuriventris* (Loew) with extensively pale tergites, which could lead to their being confused with this species. *Allognosta fuscitarsis* is evidently quite closely related to the Japanese *A. flavimaculata* Nagatomi and Tanaka. The latter species also has pale medial areas on the tergites (which are variable according to Nagatomi and Tanaka, 1969), and the male genitalia are extremely similar in the two species. I initially thought they might be conspecific, but I subsequently examined a female paratype from the United States National Museum of Natural History, through the kindness of Willis Wirth. The female genitalia are quite different, and the species is larger, has darker legs, a dark first antennal segment, and no bare area on the mesopleuron.

Allognosta obscuriventris (Loew)

Metoponia obscuriventris Loew, 1863: 299.
Metoponia similis Loew, 1863: 299. NEW SYNONYMY.

Type Material. The female type of *Metoponia obscuriventris*, from "D.C.," is housed in the Museum of Comparative Zoology (MCZ 12535), and is in perfect condition.

There are two specimens labeled as types of *Metoponia similis* Loew, also in the Museum of Comparative Zoology (MCZ 12534). One specimen bears Loew's handwritten label "similis, m.," and the other bears a label "New York, Schaum," the type locality and collector included in Loew's original description. There is no indication in the original description as to how many specimens Loew saw. Both of the above specimens are males, the only sex which Loew described. One specimen has bluish reflections on the mesonotum, a primary character used by Loew to characterize *M. similis*, and I hereby designate it as lectotype. It is labeled "Loew Coll./ similis, m./ Type 2 12534/ LECTOTYPE Metoponia similis Loew, 1863 des. N. E. Woodley, 1979/ Allognosta obscuriventris (Loew) det. Woodley 1980." The third antennal segments are missing, and the left wing is somewhat crumpled, but it is otherwise in good condition. I am designating the other specimen as paralectotype, and it is labeled "New York, Schaum/ Loew Coll./ Type 12534/ PARALECTOTYPE Metoponia similis Loew, 1863 des. N. E. Woodley 1979/ Allognosta fuscitarsis (Say) det. Woodley 1978." The entire head and left front leg are missing from the specimen.

Diagnosis. Male specimens of *Allognosta obscuriventris* (Loew) are best identified by the shape of the genitalia, particularly the long but shallowly emarginate medial process of the ventral bridge of the gonocoxites (Fig. 28), and the large gonostyli which are somewhat expanded apically, and sharply pointed.

Females are best identified by their dark pleura and the wholly pollinose ventral portion of the mesopleuron. Other diagnostic characters include the elongate antennal flagellum with the first flagellomere being short (Fig. 5), the rather poorly contrasting stigmal area of the wing, and the long and usually dark facial hairs.

Description. Male. Head black, frons with small medial longitudinal groove; ocellar tubercle slightly prominent; frons and face strongly grayish white pollinose, rest of head much more thinly pollinose; vertex, frons, face, and genal regions pilose, pile of face about 1.5 times as long as first antennal segment, longer on genae, mostly brownish but some pale hairs usually present on genae; eyes with extremely short, sparse hairs; antennae about 0.7 times length of head, dark brown with apex of second segment and first and second flagellomeres yellow, sometimes first and second antennal segments wholly yellow; first flagellomere shorter than the following three combined; longer hairs of antennae black; palpi with first segment yellowish to black, second velvety black, both segments with a mixture of pale and dark hairs; proboscis yellowish. Thorax with mesonotum shiny black, often with somewhat bluish or greenish metallic reflections, densely punctate; humeri light to dark brown, postalar calli brownish to yellowish; pleura concolorous with mesonotum, except that area below wing base is more brownish; pleura pollinose except for bare areas on extreme dorsal and posterior part of mesopleuron, entire sternopleuron except for a dorsal band, and entire pteropleuron and metapleuron; thoracic pile erect, long and pale, a few darker hairs sometimes present on mesonotum; legs with coxae yellowish to brown; remainder brownish with yellow coloration on apical one-fifth of front femora, extreme apices of middle and hind femora, basal one-third of front tibiae, extreme bases of middle and hind tibiae, basal two tarsomeres of middle legs, and basal three tarsomeres of hind legs; ranging in some specimens to more extensively yellow, only faint medial portions of hind femora and most of hind tibiae brownish, with tarsomeres colored as above except for yellowish bases of front basal tarsomeres; wings very slightly infuscated anteriorly, decreasing posteriorly, stigma distinct but weakly contrasting with wing membrane; halter yellowish brown to dark brown. Abdomen ranging from yellowish, except for lateral margins of tergites and sternites one to five and segments posterior to five brown, to totally brownish, the latter condition being found in most specimens; abdomen thinly pollinose (less so ventrally), except along dorsolateral margins, with first abdominal segment rather strongly pollinose both dorsally and ventrally; pilosity short and sparse both dorsally and ventrally, longest along lateral margins; hypopygium becoming yellowish on gonostyli and cerci; genitalia (Figs. 24–28) with median process of ventral bridge of gonocoxites produced, shallowly emarginate (Fig. 28); gonostyli expanded apically, sharply pointed; aedeagal complex (Figs. 25, 26) with lateral valves apically reflexed, slightly longer than aedeagus. Length 4.1 to 5.7 mm.

Female. Differs from male as follows: head brownish to black, frons 0.31 to 0.44 width of head, margins parallel to slightly convergent toward antennae; frons separated into two portions by a transverse sulcus which is obsolete medially; a longitudinal groove separates the lower frons into two halves, each of which is surrounded by a border of silvery gray pollinosity, medial portions impunctate and shiny to sparsely pubescent with very short hairs, and slightly convex; upper frons rather evenly punctate, with a vaguely defined medial depression which may extend longitudinally almost the length of the frons; upper frons clothed with short, pale hairs subequal in length to the first antennal segment; face silvery

gray pollinose; ocelli vaguely prominent; occipital margin rather sharp; vertex pollinose except lateral to ocelli, and above and posterior to the middle of the eye. Thorax with hairs shorter than in male. Abdomen sometimes a little less densely pollinose than in male; genitalia (Figs. 29, 30) with median aperture of furca pointed anteriorly, large; anterolateral margins ranging from nearly straight to strongly emarginate. Length 4.0 to 5.4 mm.

Distribution (Map 3). Southern Manitoba east to southern Quebec, south through Kansas, Mississippi, to Florida. A record from Colorado needs substantiation.

Locality Records (194 males, 206 females). CANADA: *Manitoba:* 5 mi. SW of Shilo. *Ontario:* Black Rapids; Cayuga; Chatham; Crozier; Eagle River; Emo; Jock River; Leamington; Marmora; Mer Bleu, 5 mi. E of Ottawa; Pt. Pelee; 10 mi. SE of Renfrew; Stittsville; Tillsonburg; Vernon. *Quebec:* Abbotsford: Aylmer; Fabre; Fairy Lake; Harrington Lake, Gatineau Park; Kazabazua; Knowlton; Laniel; Montreal; Old Chelsea. UNITED STATES: *Colorado:* Boulder Co., Valmont Butte, 5300 ft. *Connecticut:* Hartford Co.; Litchfield Co. *District of Columbia:* Washington. *Florida:* Alachua Co.; Calhoun Co.; DeSoto Co.; Highlands Co.; Marion Co.; Orange Co.; Pinellas Co.; Polk Co. *Georgia:* Clarke Co.; Fulton Co.; Liberty Co.; Lynn Co.; Rabun Co. *Illinois:* Kappa; LaRue; Spring Grove; Champaign Co.; Cook Co.; Jo Daviess Co.; Lake Co.; McHenry Co.; McLean Co.; Macoupin Co.; Peoria Co.; Union Co.; Vermilion Co. *Indiana:* Tippecanoe Co.; Wells Co. *Iowa:* Camp Dodge; Boone Co.; Story Co. *Kansas:* Miami Co.; Pottawatomie Co. *Kentucky:* Breathitt Co.; Fayette Co. *Maryland:* Prince Georgés Co. *Massachusetts:* Sherborn; Essex Co.; Hampden Co.; Middlesex Co.; Norfolk Co. *Michigan:* Branch Co.; Clinton Co.; Eaton Co.; Gladwin Co.; Ingham Co.; Ionia Co.; Livingston Co.; Midland Co.; St. Clair Co.; Wayne Co. *Minnesota:* Carver Co.; Clay Co.; Fillmore Co.; Goodhue Co.; Hennepin Co.; Houston Co.; Mille Lacs Co.; Nicollet Co.; Olmstead Co.; Pine Co.; Pipestone Co.; Ramsey Co. *Mississippi:* Lafayette Co. *Missouri:* Callaway Co. *Nebraska:* Antelope Co. *New Hampshire:* Grafton Co. *New Jersey:* Burlington Co.; Camden Co.; Gloucester Co. *New York:* Erie Co.; Greene Co.; Herkimer Co.; Steuben Co.; Tompkins Co. *North Carolina:* Graham Co.; Johnston Co.; Pender Co.; Wake Co. *Ohio:* Butler Co.; Clinton Co.; Delaware Co.; Erie Co.; Franklin Co.; Greene Co.; Tuscarawas Co. *Pennsylvania:* Cumberland Co.; Dauphin Co.; Lancaster Co.; Philadelphia Co. *Tennessee:* Hamilton Co.; Montgomery Co.; Sevier Co.; Shelby Co. *Virginia:* Chain Bridge; Maywood; Chesterfield Co.; Fairfax Co.; Giles Co.; Montgomery Co.; Shenandoah Co. *Wisconsin:* Dane Co.; Pierce Co.; Polk Co.; Sauk Co.

Flight Period. Specimens have been collected on dates ranging from 15 February (Florida) to 11 August. Collection dates, even from northern areas of the range, predominate in May and June, with only a few records from July and August. More southern regions have collection dates predominating in March and April, tapering off in May.

Biology. The immature stages of this species are not known. Adults have been collected in Malaise traps and by sweeping vegetation. Plants from which specimens have been collected include *Abies balsamea* (Ontario), alfalfa (Minnesota), raspberries (New York), and *Vibernum edulae* (Manitoba).

Remarks. This species is less common than *A. fuscitarsis*, but not nearly as rare as *A. brevicornis*. The identity of the species has not been well established in the past, due to the variable nature of its color. Specimens with metallic reflections on the mesonotum and pale medial areas on the abdominal tergites have

been known as *A. similis* (Loew). The lectotype specimen is evidently teneral, and specimens with this paler coloration may well be freshly emerged, and may darken with age. Variation in the abdominal coloration is prevalent in females of *A. fuscitarsis*, and dark specimens have been misidentified as *A. obscuriventris*. The mesopleural pollinosity is a much more reliable character for the separation of *A. obscuriventris* from *A. fuscitarsis*, as noted in the diagnosis for each species. Some variation has also been noted in the genitalia of both sexes, but particularly in the females. The male gonostyli vary to some degree in size; the range is shown in Figures 27 and 28. The usual size is nearer to the larger example. The overall width of the genital capsule is somewhat variable, as is the length of the space between the gonocoxal apodemes and the main part of the gonocoxites. The overall form of the genitalia is distinctive however, and I have examined a fair number of individuals in the course of determining the status of *A. similis*. I have no reason to suspect that more than one species is involved. The female genital furca is also variable. In particular, the anterolateral margins of the sternite are variable, ranging from nearly straight to deeply emarginate. The most constant feature seems to be the shape of the median aperture, which is pointed anteriorly. However, the one female specimen examined from Colorado has the aperture with the anterior margin rather straight, as in *A. fuscitarsis*. More material needs to be collected from this region before this variant can be interpreted properly. I have figured two specimens with female genitalia representing the extremes observed (Figs. 29, 30). A more extensive study may indicate that the female genitalia of this species are more variable than presently believed, and are not useful for separating *A. obscuriventris* from *A. fuscitarsis* in every case. They seem to be reliable in most cases, however, and corroborate other characters that have proved to be useful in separating these two taxa.

Genus BERIS Latreille

Beris Latreille, 1802: 447; type species *Stratiomys sexdentata* Fabricius (=*Musca chalybata* Forster), by monotypy.

Hemiberis Enderlein, 1921: 209; type species *Beris quadridentata* Walker (=*Beris fuscipes* Meigen), by original designation. NEW SYNONYMY.

Diagnosis. Members of the genus *Beris* may be distinguished from all other North American Beridinae by their extremely small, one-segmented maxillary palpi. Other generic features include medium size with elongate body form, and rather uniformly distributed pilosity; eyes pilose in both sexes; males holoptic; females dichoptic, with wide frons with nearly parallel margins; antennal flagellum more or less conical, usually eight-segmented (seven in *B. strobli*); oral margin somewhat produced ventrally; thorax metallic greenish in Nearctic species; scutellum usually with six spines, sometimes eight, progressively smaller laterally, sometimes irregular; legs with hind pair elongate, the basitarsus of hind leg inflated in male; middle tibiae without apical spur; wings with R_4 present, R_{2+3} arising basal to r-m, M_1 and M_2 sometimes petiolate to separate at discal cell, M_3 absent; abdomen brownish, tergites two to six with preapical transverse grooves, that of tergite six faint.

The new synonymy of *Hemiberis* Enderlein with *Beris* rather than with *Actina* is based upon the lectotype designation for *Beris quadridentata* Walker, which is discussed below.

The Nearctic species of *Beris* have remained rather poorly understood until now. The genitalia of both sexes, which offer the best diagnostic characters, have not been previously examined in detail nor figured for our species. I examined these structures, and they have indicated the presence of a third species never before recorded from North America, and one synonymy with a Palaearctic species.

In addition, examination of the holotypes has revealed one further synonymy. Thus there are three Nearctic taxa known at present, two of which are also widely distributed in the Palaearctic Region. The genus as a whole is more diverse in the Old World, being found in the Palaearctic and northern Oriental Regions. Species referred to *Beris* in the Southern Hemisphere belong in other genera. Despite examination of numerous Beridinae from the Southern Hemisphere, I have never seen specimens which are congeneric with true *Beris*, which is apparently restricted to the Northern Hemisphere. Most of the southern species have only four scutellar spines and all have well-developed two-segmented palpi.

The life histories of the North American species are poorly known. The larvae have never been collected (or at least associated with adults), and the only knowledge of the immature stages for our species is based upon European work. Males probably form conspecific swarms, for this behavior has been recorded anecdotally for British species (Verrall, 1909). Males have large, holoptic eyes and larger ommatidia dorsally, although they are not clearly divided from the smaller, lower ones. This is commonly believed to be an adaptation coupled with swarming behavior (McAlpine and Monroe, 1968; Downes, 1969). The enlarged hind basitarsus of male *Beris* may also function in some connection either with swarming or associated mating behavior.

KEY TO THE NEARCTIC SPECIES OF *BERIS*

1. Males (holoptic) 2
   Females (dichoptic) 4
2. Tenth tergite with posterolateral surstyli (Fig. 33); aedeagus long, arcuate, the aedeagal valves subequal in length to the aedeagus (Fig. 34); posteromedial area of ventral bridge of gonocoxites feebly produced (Fig. 36) ..... *fuscipes* Meigen
   Tenth tergite truncate posteriorly, without surstyli (Figs. 37, 41); aedeagal valves either longer or shorter than the aedeagus itself (Figs. 38, 42) 3
3. Antennal flagellum seven-segmented (Fig. 9); medial region of ventral bridge of gonocoxites strongly produced (Fig. 44); aedeagus much shorter than aedeagal valves (Fig. 42) ..... *strobli* Dušek & Rozkošný
   Antennal flagellum long, eight-segmented (Fig. 7); medial region of ventral bridge of gonocoxites feebly produced (Fig. 40); aedeagus longer than aedeagal valves (Fig. 38) ..... *luteipes* Johnson
4. Antennal flagellum eight-segmented (Figs. 6, 8); spermathecal ducts sclerotized posteriorly (Figs. 45, 46); median aperture of ninth sternite reduced, very small, most of furca sclerotized 5
   Antennal flagellum seven-segmented (Fig. 9); spermathecal ducts unsclerotized posteriorly (thus not shown in Fig. 47); median aperture of ninth sternite large, encompassing most of that surface ..... *strobli* Dušek & Rozkošný
5. Antennal flagellum quite conical, tapering sharply toward apex (Fig. 6); sclerotized portion of spermathecal ducts very long, twice as long as the rest of the genital segment (Fig. 45); median hind margin of furca posterior to median aperture bilobed; widespread in mountainous and boreal regions except on the Pacific coast ..... *fuscipes* Meigen
   Antennal flagellum usually long, tapering more gradually toward apex (Fig. 8); sclerotized portion of spermathecal ducts shorter, only slightly longer than the rest of the genital segment (Fig. 46); median hind margin of furca posterior to median aperture truncate; found in British Columbia, Alberta, Washington, Oregon, California, western Nevada, Idaho, and possibly Wyoming ..... *luteipes* Johnson

Beris fuscipes Meigen

Beris fuscipes Meigen, 1820: 8.
Beris brevicornis Heyden *in* Loew, 1846: 284.
Beris quadridentata Walker, 1848: 127. NEW SYNONYMY.
Oplacantha annulifera Bigot, 1887: 21. NEW SYNONYMY.
Actina canadensis Cresson, 1919: 174.
Beris annulifera var. *brunnipes* Johnson, 1926b: 109.
Beris sachalinensis Pleske, 1926: 408.
Beris fuscotibialis Pleske, 1926: 409.
Beris sychuanensis Pleske, 1926: 411.
Beris mongolica Pleske, 1926: 414.
Beris petiolata Frey, 1960: 80.

Type Material. The type of *Beris fuscipes* Meigen is housed in the Museum

National d'Histoire Naturelle, Paris. It was not available for study.

Loew (1846) first used the name *Beris brevicornis* in connection with specimens sent to him by "Hr. v. Heyden." Loew obviously used the name as a synonym of *B. fuscipes*. It is apparently only a manuscript name, never having been formally proposed; thus no type material exists.

Two syntypes of Walker's *Beris quadridentata* are housed in the British Museum. The male is probably conspecific with *Actina viridis* (Say), but is badly damaged. Thus I hereby designate the female specimen as lectotype, which bears the following labels: "♀ Type/Beris quadridentata, ♀. Walker. (Type). = B. viridis, Say (O.S.)./ one of Walkers series so named EAW; [verso reads] Beris quadridentata Walk./ LECTOTYPE Beris quadridentata Walker 1848: 127 des. N. E. Woodley 1980/ Beris fuscipes Meigen det. Woodley 1980." The specimen lacks the right antennal flagellum, the distal portion of the fifth tarsomere of the right front leg, the left middle leg, and the fifth tarsomere of the right hind leg, but is otherwise in good condition. The male specimen is designated as paralectotype, and bears identical labels except that on the first two labels "♂" replaces "♀," and the fifth label reads "Actina viridis (Say) det. Woodley 1980."

The female syntypes of *Oplacantha annulifera* Bigot are also presently housed in the British Museum. I hereby designate one as lectotype, which bears the labels "Opl. annulifera Big. Col. Big/ Octacantha [sic] annulifera Big. AMERICA ex Bigot Coll: BM 1960-539./ LECTOTYPE Oplacantha annulifera Bigot 1887 des. N. E. Woodley 1979/ Beris fuscipes Meigen det. Woodley 1979." The specimen lacks the left middle leg, the right hind leg, and the second segment of the right cercus. The second specimen that I examined, with labels identical to those of the lectotype, is hereby designated as paralectotype, and is labeled accordingly. It is conspecific with the lectotype.

The female holotype of *Actina canadensis* Cresson is housed in the Academy of Natural Sciences, Philadelphia, Pennsylvania. It is labeled as Type 6252, contrary to the published number of 6196. The specimen lacks the right front leg, but is otherwise in good condition.

The male holotype of *Beris annulifera* var. *brunnipes* Johnson is in the Museum of Comparative Zoology (MCZ 7494). It lacks the right antennal flagellum, but is otherwise in excellent condition.

Diagnosis. Males of *Beris fuscipes* Meigen may be readily recognized by the presence of posterolateral surstyli (Fig. 33) on the tenth tergite, which may or may not be curved. This character is easily visible without dissection. Females are readily recognized by their terminalia with the posterior portions of the spermathecal ducts being long and sclerotized, and the medial region of the ninth sternite posterior to the small median aperture bilobed. Both sexes have antennae with a moderately short, conical flagellum which is wide basally and which tapers strongly toward the apex (Fig. 6). The maxillary palpi, although very small as in all *Beris*, are larger in this species than in other North American forms. The differences are slight, however, and are difficult to appreciate without comparison with the other two species.

Description. Male. Head black, frons and face shiny, upper occiput pollinose; entire head including eyes pilose, color of pile variable, ranging from mostly pale with scattered dark hairs to almost wholly dark, usually a mixture of both; hairs at oral margin subequal in length to the first two antennal segments combined, those above antennae subequal to the length of the first segment; antennae black, very rarely with inner portion of first flagellomere yellowish, shorter than length of head; first two segments subequal, the second tapering to about twice width of base at apex; flagellum 1.3 to 1.7 times length of first two segments combined, basal width wider than apex of second segment, tapering strongly to a rather

sharp apex, slightly concave on inner surface; pile of antennae black; proboscis yellow; palpi minute, elongate oval; ocelli yellowish, ocellar tubercle slightly prominent. Thorax with mesonotum shiny green, often with bluish reflections, sometimes medial portion of mesonotum and scutellum bluish, very rarely brassy green; scutellum normally with six spines; pleura brownish black, upper portions with greenish reflections; thoracic pile mostly pale, sometimes with scattered dark hairs on mesonotum, length on mesonotum subequal to first two antennal segments combined; legs with front and hind coxae brownish black, middle coxae yellowish, occasionally dark; rest of legs yellowish except front and middle legs with apical halves of basitarsi and entire tarsomeres two to five dark brown, and hind legs with brownish subapical region on femora, tibiae and basitarsi slightly brownish, apical four tarsomeres dark brown; ranging in darker specimens to wholly brown except for yellowish extreme apices of all femora, basal one-thirds of front and middle tibiae, and extreme bases of hind tibiae, also bases of hind femora evanescently yellowish; wings brownish, evenly set with microtrichia, stigma darker; halter pale yellow with darker stem. Abdomen brown, evenly pollinose dorsally except for lateral margins, becoming less pollinose on apical tergites, ventrally shiny; pile pale, longest laterally; genitalia (Figs. 33–36) with gonostyli ovate, not arcuate, often yellowish; medial process of ventral bridge of gonocoxites feebly produced, truncate (Fig. 36); aedeagal complex (Figs. 34, 35) very long, strongly arcuate, lateral valves subequal in length to aedeagus; tenth tergite (Fig. 33) with well-developed surstyli, straight or curved; cerci yellowish. Length 5.0 to 6.9 mm.

Female. Differs from male as follows: head with frons and face brownish black to black; frons 0.23 to 0.35 width of head at anterior ocellus, finely punctate, occasionally with faint longitudinal striae below ocelli; a small circular depression present above antennae; pile of head pale, that of face shorter than length of first antennal segment; antennae brownish black to black, with inner portions of flagellomeres two to four slightly yellowish, ranging in pale specimens to apical portions of first and second segments, entire first and second flagellomeres, and inner portions of flagellomeres three to six yellow; pile of first two antennal segments ranging from mostly dark to mostly pale. Thorax with pale pile, shorter than in male; legs wholly yellow except for front and hind coxae, extreme apices of all basitarsi, and entire tarsomeres two to five of all legs brownish; ranging to as dark as in darkest males, except that extreme bases of all femora and all basitarsi are yellowish. Abdomen with entire first tergite, basal half of second tergite, and extreme bases of tergites three to five pollinose, remainder shiny; pile pale, shorter than in male; genitalia (Fig. 45) with sclerotized posterior portions of spermathecal ducts very long, twice as long as the genital segment itself; median aperture of genital sternite small; medial hind margin of genital sternite posterior to median aperture bilobed; cerci yellowish, first segment slightly thicker than second. Length 4.7 to 6.9 mm.

Distribution (Map 5 shows Nearctic portion). Holarctic; ranging from Great Britain east to Japan in the Palaearctic Region, and in the Nearctic Region essentially montane and boreal, from Alaska south through the Rocky Mountains to southern Arizona and New Mexico; from British Columbia east across the northern United States and Canada to Labrador, Maine, south to Tennessee.

Locality Records (190 males, 262 females). UNITED STATES, ALASKA: Anchorage; Big Delta; Brooks Lake; Curry; Eagle River; Independence Mine; Kenai Peninsula, 15 mi. SE of Anchorage; Salcha River, Alaska Highway mile 1481; Seward; Shaw Creek, Richardson Highway mile 289. CANADA: *Alberta:*

Athabasca; Banff; Bilby; Blairmore; Cooking Lake, near Edmonton; Edmonton; Gorge Creek; Gull Lake; Jumping Pond Creek, 20 mi. W of Calgary; Kananaskis; McMurray; 8 mi. E of Morley; Nordegg; Opal; Pincher; Seebe; Wabamun; Waterton. *British Columbia:* Canim Lake; Ground Hog Basin, Selkirk Mountains; Liard Hot Springs, Alaska Highway mile 496, 1500 ft.; Nass River, Aiyansh; Salmon Arm; 6 mi. W of Terrace; *Hudson Bay Territory:* no further data. *Labrador:* Parroquet Island; Straights of Belle Isle. *Manitoba:* Minnitonas; Ninette; 5 mi. SW of Shilo. *Newfoundland:* Mtns. E of Codroy; St. Anthony; Stephenville. *Ontario:* Britannia; Finland; Kearny; Low Bush, Lake Abitibi; Macdiarmid, Lake Nipigon; Maynooth; Normandale; One Sided Lake; Ottawa; Simcoe; Thornhill; Vermilion Bay. *Quebec:* Bradore Bay; Duncan Lake, near Rupert; Forestville; Gaspe; Hull; Knob Lake, 54°47′, 66°47′; Laniel; Megantic; Mistassini; Old Chelsea; Rupert House. *Saskatchewan:* Kenosee. *Yukon:* Dawson; 14 mi. E of Dawson, 1500 ft.; Dempster Highway mile 87; Sheldon Lake, 131°37′, 62°56′, 3500 ft. UNITED STATES: *Arizona:* Colter's Ranch, White Mts.; Graham Co. *Colorado:* Blackhawk; Buckhorn Creek; Green Mt. Falls, 8000 ft.; Sierra Blanca, 11,500 ft.; Costilla Co.; Grand Co.; Gunnison Co.; Larimer Co.; Rio Grande Co.; Teller Co. *Idaho:* Latah Co. *Maine:* Penobscot Co. *Michigan:* Cheboygan Co.; Chippewa Co. *Minnesota:* Anoka Co.; Clearwater Co.; Cook Co.; Lake Co.; Pope Co.; Ramsey Co. *Montana:* Avalanche Lake, Glacier Park; Gallatin Co.; Missoula Co. *New Hampshire:* Pinkham Notch; White Mts.; Carroll Co.; Coos Co. *New Mexico:* Therma; Otero Co.; Sandoval Co.; Taos Co. *New York:* Essex Co.; Greene Co. *Oregon:* Baker Co. *Tennessee:* Indian Gap, 5200 ft., Great Smoky Mountains National Park; Sevier Co. *Utah:* Cache Co.; Grand Co.; Uintah Co. *Vermont:* Caledonia Co. *Washington:* Columbia Co. *Wisconsin:* Florence Co.; Vilas Co. *Wyoming:* Albany Co.

Flight Period. Collection dates range from 12 May to 11 August. Almost all specimens were collected in June and July.

Biology. The larva of *Beris fuscipes* was briefly described by Lenz (1923), and was collected under bark. Larvae have not been collected in North America to my knowledge. Adults apparently occur in situations similar to those of other species. I have seen series of *B. fuscipes* and *B. strobli* collected at the same locality on the same date. Specimens have been taken by sweeping, in Malaise traps, and at light. One label also reads "in marsh clearing" (British Columbia). Records attributed to this species referring to their being collected on flowers (McFadden, 1972) actually refer to *B. luteipes*. Males probably form conspecific swarms, for reasons discussed above.

Remarks. I have been unable to examine the type of *Beris fuscipes.* It was apparently last examined by Verrall (1909), who stated that the specimen was a male. It needs to be reexamined, however, particularly with reference to the genitalia. I have also not examined the various types for synonyms based on Palaearctic material, for these have been adequately treated by Rozkošný (1973) and Nartshuk and Rozkošný (1975, 1976), who have cleared up much of the synonymy that has accumulated for the Palaearctic species. These workers have also provided figures of the male genitalia which have proved very useful in determining the status of the Nearctic species of *Beris*.

Beris fuscipes has long been called *B. annulifera* in North America. The work cited in the previous paragraph led me to discover the synonymy of this name with *B. fuscipes*. I examined European specimens of the species and determined that our material was conspecific, and confirmed the synonymy by examining the original Bigot type material. The types

were stated as being from Georgia, but labels on the specimens indicate only "America," and I have not seen modern material from Georgia, although it may occur in the northern part of the state.

I have also examined the type material for *Beris quadridentata* Walker. The male specimen, upon which previous synonymy with *Actina viridis* (Say) has been based, is badly damaged. I therefore have designated the female, which is in much better condition, as lectotype. It is conspecific with *Beris fuscipes* (Walker states that the female has six scutellar spines, indicating a *Beris*, and I have examined the terminalia to confirm the identity of the lectotype). This has resulted in two changes in synonymy. The genus *Hemiberis* Enderlein, which was based upon *B. quadridentata* as type species, becomes a junior synonym of *Beris* rather than of *Actina* as it has been in the past. And *Beris quadridentata* becomes a synonym of *B. fuscipes*. Because the lectotype designation does not affect any name presently in use, and is very unlikely to do so in the future, I felt it was more advisable to designate a specimen as lectotype that could be positively identified. The damaged male lacks most of the abdomen, including the genitalia. Thus, if another species of *Actina* is discovered in the future from the Nearctic Region, it would be difficult to determine the identity of *B. quadridentata* if the male was the lectotype, even though at present it can be assigned to *Actina viridis* (simply because there is only one Nearctic *Actina*). Therefore, I feel the above solution is most likely to result in future stability of all names concerned.

The female type of *Actina canadensis* Cresson was also examined, and I concur with McFadden (1972), who synonymized it with *B. annulifera*, that it is not specifically distinct. I likewise could not detect the "steel blue vittae" first reported by Curran (1927). I also agree with McFadden that *Beris annulifera* var. *brunnipes* Johnson is merely a variant not warranting subspecific recognition, and I have confirmed that synonymy by examining the holotype.

Beris fuscipes is the most widespread species of the genus in the Nearctic Region, being found in boreal and mountainous regions across the continent. It is fairly variable, particularly with respect to leg coloration. The coloration of the legs was briefly studied by McFadden (1972), who determined that it did not vary in any way distinctly correlated with geographical regions. It is interesting to note that two paratypes, one each of *B. annulifera* var. *luteipes* and *B. a.* var. *brunnipes*, were collected from the same locality in New Hampshire. Thus it is not feasible to maintain subspecific taxa for this species.

There has been some variation detected in the shape and size of the male tenth tergite. In some specimens, particularly from Washington and Idaho, the tergite is small and the surstyli are quite straight, rather than being curved as in most specimens. These variations are minor however, and other features of the male genitalia are quite constant and distinctive.

The female terminalia were illustrated by Nagatomi and Iwata (1978). The preparation was not dissected, however, so that the structures of the genital furca are not well depicted. These structures are quite diagnostic for the species of *Beris* in North America, and are illustrated here for the first time.

Beris luteipes Johnson

Beris annulifera var. *luteipes* Johnson, 1926b: 109. NEW STATUS.
Beris californica James, 1939: 546. NEW SYNONYMY.

Type Material. The holotype of *Beris annulifera* var. *luteipes* Johnson, from Seattle, Washington, is presently housed in the Museum of Comparative Zoology (MCZ 7493). The specimen is a male, and is lacking both third antennal segments, the left middle leg, both hind

legs, and most of the left wing. The female allotype is conspecific, and is also from Seattle. All of the paratypes are *Beris fuscipes* Meigen.

The holotype of *Beris californica* James, from Del Norte Co., California, is presently housed in the collection of the Abteilung Taxonomie der Insekten des Institutes für Pflanzenschutzforschung der Akademie der Landwirtschaftswissenschaften der DDR, Eberswalde, East Germany. The male specimen is missing the left middle leg, but is otherwise in excellent condition.

Diagnosis. Males may be separated from other species of *Beris* occurring in North America by their genitalia, especially the combination of the truncate tenth tergite (Fig. 37), the long aedeagus (Figs. 38, 39), and the feebly produced process of the ventral bridge of the gonocoxites (Fig. 40); females may be recognized by their short but sclerotized posterior portions of the spermathecal ducts, which are only about as long as the ninth sternite, the truncate medial hind margin of the genital sternite posterior to the small median aperture (Fig. 46), and the elongate, slender antennal flagellum (Fig. 8). In much of its range it is the only species of *Beris*.

Description. Male. Head black, frons and face shiny, upper portion of occiput pollinose, entire head including eyes pilose; pile black, occasionally with intermixed pale hairs below antennae; hairs at oral margin subequal to, to considerably longer than, the first two antennal segments combined, those above antennae subequal to the first antennal segment, occasionally slightly longer; antennae black, occasionally with extreme apex of second segment, and inner portions of flagellomeres one to five yellowish; length ranging from shorter than the length of head to subequal to it, first two segments subequal, second widened apically; flagellum long and slender, 1.8 to 2.2 times length of the first two segments combined (Fig. 7), base subequal in width to the second segment, occasionally slightly wider; longer pile of antennae black; proboscis yellow; palpi minute, elongate-oval; ocelli yellow, ocellar tubercle somewhat prominent. Thorax with mesonotum shiny metallic green to blackish green, sometimes with brassy reflections; pleura blackish, dark brownish below wing base, often with greenish reflections, particularly on mesopleuron and sternopleuron; scutellum concolorous with mesonotum, normally with six spines; pile ranging from dark with a few scattered pale hairs to entirely pale, about length of first two antennal segments combined, to somewhat longer; legs with front and hind coxae blackish, middle coxae mostly yellowish; rest of legs wholly yellow except for brownish black coloration on apical third of basitarsi and entire tarsomeres two to five of front and middle legs, and last four tarsomeres of hind legs; ranging in some specimens to yellow except for wholly brownish apices of front and middle femora, hind femora entirely brownish, darker at apices, front and middle tibiae brown except for basal one-thirds, hind tibiae dark brown except for basal one-fifths, and all tarsi wholly brown; wings brownish, stigma darker, evenly set with microtrichia; halter ranging from wholly yellowish to wholly brownish. Abdomen brown to blackish brown, dorsally subshining, evenly and finely pollinose, ventrally shiny; pile ranging from wholly pale to blackish dorsally and laterally, the remainder pale, longest laterally; genitalia concolorous with abdomen, but often with gonostyli and cerci yellowish; gonostyli ovate, not strongly arcuate; posteromedial region of ventral bridge of gonocoxites truncate and feebly produced (Fig. 40); aedeagal complex (Figs. 38, 39) with aedeagus longer than lateral valves; tenth tergite truncate posteriorly, without surstyli (Fig. 37). Length 5.3 to 6.6 mm.

Female. Differs from male as follows: head with frons and face brownish black

to black, shiny, sometimes with bluish or greenish reflections; frons 0.28 to 0.37 width of head at anterior ocellus, finely punctate, with small round depression above antennae, rarely with faint longitudinal striae below ocelli; pile of head pale, very rarely darker below antennae, that of face at most the length of the first antennal segment; antennae black with apex of second segment and inner portion of basal flagellomere yellow, ranging to having yellow coloration on apex of first segment, entire second segment, entire first flagellomere, and inner portions of flagellomeres two to six; hairs of first two antennal segments ranging from entirely pale to entirely black; flagellum 2.0 to 2.5 times length of first two antennal segments combined (Fig. 8). Thorax with mesonotum shiny green, more often with bluish reflections than in male, pleura often more extensively brownish; pile usually pale, shorter than in male; legs with hind coxae sometimes yellow, femora and tibiae yellow, apex of hind femora may be evanescently brownish. Abdomen dark to light brown; tergites with most of segments one and two, and basal portions of three, four, and five pollinose, rest shiny; pile pale, shorter than in male; genitalia yellowish, posterior portions of spermathecal ducts sclerotized but short, about the length of the genital segment itself (Fig. 46); median aperture of genital sternite small, medial hind margin behind aperture truncate; cerci yellowish, first segment thicker than terminal segment. Length 4.7 to 6.6 mm.

Distribution (Map 4). This species is endemic to the Nearctic Region, and is found from British Columbia south to California and extreme western Nevada, east to Alberta and Idaho. A record from northwestern Wyoming needs confirmation.

Locality Records (95 males, 103 females). CANADA: *Alberta:* Waterton. *British Columbia:* Bevan, Vancouver Island; Crowsnest; Duncan, Goldstream, Vancouver Island; Hope, Silver Lake; Hot Springs, 5 mi. S of Lakelse; Mission City; Osoyoos, Anarchist Mtn.; Terrace; Tyee, 27 mi. E of Prince Rupert. UNITED STATES: *California:* Del Norte Co.; Los Angeles Co.; Nevada Co.; San Bernardino Co.; San Mateo Co.; Siskiyou Co.; Trinity Co. *Idaho:* Clearwater Co.; Latah Co. *Nevada:* Ormsby Co. (W of Carson City). *Oregon:* Benton Co.; Clackamas Co.; Curry Co.; Douglas Co.; Hood River Co.; Jefferson Co.; Marion Co.; Tillamook Co.; Washington Co. *Washington:* Chelan Co.; Clallam Co.; Clark Co.; King Co.; Lewis Co.; Mason Co.; Okanogan Co.; Pacific Co.; Skamania Co.; Snohomish Co.; Spokane Co.; Whitman Co.; Yakima Co.

One further locality seems doubtful: *Wyoming:* Yellowstone Park, Clematis Creek. Further collecting may substantiate the presence of *B. luteipes* that far east, but in light of what is currently known of its distribution, it seems unlikely. Thus this single male specimen, which I have examined, may be mislabeled.

Flight Period. Specimens of this species have been collected as early as 20 May, and as late as 2 August, with the vast majority of records from June and July.

Biology. The immature stages of this species remain unknown. Adults have been collected in Malaise traps, both unbaited and baited with CO_2. I have collected females in low vegetation along a small, open stream at moderate elevation in Washington. Label data indicate collections from "marshy lake and stream margin," "plants in swamp," and "plants along river." The species has also been collected from flowers of *Heracleum lanatum* and "Umbelliferae" (both from British Columbia). The latter record was cited by McFadden (1972) under *Beris annulifera* (=*B. fuscipes*); I have examined the specimen seen by him, and it was misidentified.

Remarks. This species has been known as *Beris californica* since it was first discovered to be specifically distinct by

James (1939). Examination of the holotype of *Beris annulifera* var. *luteipes* Johnson, originally described as a variety, but subsequently recognized as a subspecies by James (1965), indicated that it was a distinct species, conspecific with *B. californica* rather than with *B. fuscipes*. This was subsequently confirmed by examination of the holotype of *B. californica*. *Beris luteipes* thus becomes the valid name for the taxon by priority. McFadden (1972) synonymized the variety with *B. annulifera* (=*B. fuscipes*), and indeed Johnson's original series was mostly that species, but the holotype male is clearly conspecific with *B. californica*. The holotype was collected at Seattle, Washington, which is outside the range of *Beris fuscipes*. I can only conclude that McFadden did not examine the holotype to substantiate his synonymy.

Beris luteipes is the only species in the genus that is endemic to the Nearctic Region. It must be pointed out, however, that the structure of the genitalia indicates a close relationship with *Beris heptapotomica* Pleske (see Nartshuk and Rozkošný, 1975) which is known from the USSR, and *Beris* sp. A of Nagatomi and Tanaka (1972). I have not examined specimens of either of these taxa. Nartshuk and Rozkošný have noted the similarity of *B. heptapotomica* to *Beris* sp. A.

Females from the area of distributional overlap with *B. fuscipes* can be difficult to determine with certainty. The length of the antennal flagellum is somewhat variable, but it is usually not as wide basally as that of *B. fuscipes*, nor is it generally as short. The range of overlap between *B. luteipes* and *B. fuscipes* is not yet well understood, and if the record of the former from Wyoming that now appears doubtful is substantiated the region may be larger than is presently anticipated. Thus, it is desirable to check the genitalia of females not associated with males to identify them positively. The genitalia are relatively invariable, and are quite diagnostic at the specific level, but unfortunately are not visible without dissection.

Coloration of the legs, pilosity, and to some extent the mesonotum, is variable in this species. The length of the antennal flagellum is somewhat variable, and is sexually dimorphic (Figs. 7, 8), that of the males being shorter and more compact. In general, the palest specimens, and those with the longest antennal flagella, have been recorded from California.

Beris strobli Dušek and Rozkošný

Beris chalybeata var. *obscura* Strobl, 1909: 47 (preoccupied by *obscura* Meigen, 1820: 4).
Beris strobli Dušek and Rozkošný, 1968: 294 (new name for *obscura* Strobl).
Beris latifascies Nagatomi and Tanaka, 1972: 100.

Type Material. The holotype female of *Beris chalybeata* var. *obscura* Strobl is in the Strobl collection, presently housed at the Institutes für Pflanzenschutzforschung in Eberswalde, East Germany, in the care of G. Morge. It is in poor condition, missing the left antenna, the flagellum of the right antenna, the two apical tarsomeres of the left front leg, the apical tarsomeres of the right middle leg, the entire hind legs, the left wing, and the abdomen.

Diagnosis. Males can be told easily by the structure of the genitalia: the gonostyli are large and strongly arcuate, and the medial process of the ventral bridge of the gonocoxites is well developed and bilobed (Fig. 44). Females are difficult to determine positively, except by use of the genitalia, which have the spermathecal ducts unsclerotized posteriorly, and the median aperture of the genital sternite very large (Fig. 47). Both sexes have compact, short, conical antennal flagella, which taper gradually toward the apex, and are composed of seven segments (Fig. 9), although this is difficult to detect. The palpi are very small, and also quite difficult to observe; this character can be used to some extent to separate females from *B.*

fuscipes, which has larger (although still minute) palpi.

Description. Male. Head brownish black to black, frons and face shiny, upper occiput pollinose; entire head including eyes pilose, pile mostly black, but pale hairs may be intermixed below antennae; hairs at oral margin about the length of the first two antennal segments combined, those of frons about the length of the first segment; antennae (Fig. 9) shorter than the length of head, black, first two segments sometimes brownish; scape and pedicel subequal in length; flagellum compact, blunt conical, about 1.7 times as long as the first two segments combined, composed of seven flagellomeres; pile of antennae black; proboscis yellow; palpi very minute, more or less spherical; ocelli yellowish, ocellar tubercle somewhat prominent. Thorax with mesonotum somewhat shiny, metallic greenish; pleura brownish to blackish, dorsal sclerites sometimes with greenish reflections; scutellum concolorous with mesonotum, normally with six spines; pile of thorax yellowish to brownish, about half the length of antennae; legs brownish black with apices of femora and basal one-fourth to one-third of all tibiae yellow; ranging in some specimens to mostly yellow except front and hind coxae, apices of all basitarsi, and entire distal four tarsomeres of all legs brownish; wings brownish, stigma darker, evenly set with microtrichia; halter yellow, sometimes with apex of stem and base of knob brown. Abdomen brownish, tergites subshiny, very finely pollinose; sternites shiny; pile pale, longest laterally; genitalia (Figs. 41–44) brown, gonostyli large, arcuate, yellowish; posteromedial portion of ventral bridge of gonocoxites strongly produced, bilobed (Fig. 44); aedeagal complex (Figs. 42, 43) arcuate, aedeagus much shorter than lateral valves; tenth tergite (Fig. 41) truncate posteriorly, without surstyli. Length 5.3 to 6.2 mm.

Female. Differs from male as follows: head brownish to brownish black; pile of head mostly pale, short, at most the length of the first antennal segment; frons at anterior ocellus 0.29 to 0.37 width of head, slightly to distinctly longitudinally striate below ocelli, slightly depressed just above antennae; antennae brownish to black, with apex of second segment and flagellum with inner portions of flagellomeres one and two (sometimes ranging as far as the sixth), yellowish; hairs of antennae pale to brownish, those at apex of flagellum black. Thorax with mesonotum sometimes more brilliantly metallic than in male; pile shorter, pale; legs rarely as dark as in most males, often wholly pale yellow with apical tarsomeres brownish. Abdomen brownish, shiny, terminal segments sometimes slightly paler; cerci with first segment thick, second much thinner, deflated when dry, thus appearing laterally compressed; genitalia (Fig. 47) with spermathecal ducts unsclerotized posteriorly (thus not shown in Fig. 47); median aperture of genital sternite very large; medial hind margin of genital sternite posterior to aperture feebly bilobed. Length 4.9 to 5.9 mm.

Distribution (Map 4 shows Nearctic portion). Holarctic; from western Europe east to Japan in the Palaearctic Region (Nartshuk and Rozkoský, 1976: 132, map); from Alaska east to Ontario, Wisconsin, and Minnesota in the Nearctic Region.

Locality Records (24 males, 29 females). UNITED STATES: ALASKA: 15 mi. SE of Anchorage; Big Delta, Lake Boleo; Richardson Highway mile 315; Salcha River, Alaska Highway mile 1481; Shaw Creek, Richardson Highway mile 289; Unalakleet. CANADA: *Alberta:* Bilby; Edmonton; Gull Lake; Jumping Pond Creek, 20 mi. W of Calgary; McMurray; Wabamun. *British Columbia:* Atlin, 3000 ft.; Ft. Nelson; Liard Hot Springs, Alaska Highway mile 496, 1500 ft. *Manitoba:* 5 mi. SW of Shilo. *Northwest Territories:* Ft. McPherson; Norman Wells. *Ontario:* Macdiarmid, Lake Nipigon; One Sided Lake. *Yukon:* Dawson; LaForce, 132°20′, 62°41′, 3300 ft.; North Fork Crossing,

Peel Plt. Road mile 43, 3500 ft.; Rampart House; Swim Lakes, 133°, 62°13′, 3200 ft. UNITED STATES: *Minnesota:* Cool Co., Grand Marais. *Wisconsin:* Door Co.

Flight Period. Collection dates range from 28 May to 28 July. All specimens except the one May record were taken in June and July.

Biology. The immature stages of this species have not been collected. Adults have been collected from vegetation, notably "swept ex *Equisetum* sp." (Manitoba) and from *Salix* (Yukon). The former record was previously attributed to *Beris fuscipes* (as *B. annulifera*) by McFadden (1972), but reexamination of that specimen has shown it to be this species.

Remarks. This species has not previously been reported from the Nearctic Region. This is surprising, since some male specimens have been previously determined as *Beris annulifera* (=*Beris fuscipes*), yet they completely lack the surstyli of the tenth tergite which are easily visible externally on male specimens of *B. fuscipes*. Specimens of *B. strobli* are not common in North American collections, probably because the species is primarily an inhabitant of far northern areas that are seldom collected.

I have examined the type of *B. chalybeata* var. *obscura* Strobl. While it is so badly damaged now that it is difficult to be sure of its identity, I am following the synonymy established in the literature by Dušek and Rozkošný (1968). Through the kindness of Rudolf Rozkošný, I was able to examine other European specimens of *B. strobli*, and was able to confirm the conspecificity of Nearctic material. Nartshuk and Rozkošný (1976) proposed the synonymy of *B. latifascies* Nagatomi and Tanaka, described from Japan. I have not yet examined the holotype of that taxon.

This species is likely to be confused only with *Beris fuscipes*, with which it is widely sympatric in northern regions. Males are easily determined by their genitalia, which are visible externally. But females are difficult to identify with certainty unless specimens of both species can be compared. With single female specimens it is necessary to examine the internal genitalia. But external characters sometimes of use include the frons, which tends to be wider in *B. strobli* than in specimens of *B. fuscipes*, and definite longitudinal striations are usually present on the frons below the ocelli. These two characters do overlap to some degree in the two species, however. The antennal flagellum is distinctive for each species, but this is difficult to appreciate without having seen both. The flagellum is only seven-segmented in *B. strobli*, which has not been noted in the past. This is difficult to ascertain without clearing the flagellum. Specimens of both *Beris fuscipes* and *B. strobli* have been collected at the same locality on the same date, so overlap of ranges definitely occurs at the local level. Thus for positive identification of females, it is best to examine the genitalia.

Beris strobli probably does not occur in sympatry with *Beris luteipes*, except possibly in southeastern British Columbia or southwestern Alberta. They have not as yet been recorded from the same locality.

Genus EXODONTHA Rondani

Exodontha Rondani, 1856: 169; type species *Exodontha pedemontana* Rondani (=*Beris dubia* Zetterstedt), by original designation.

Hexodonta, emend.

Acanthomyia Schiner, 1860: 49; type species *Beris dubia* Zetterstedt, by original designation.

Scoliopelta Williston, 1885: 152; type species *Scoliopelta luteipes* Williston, by monotypy.

Diagnosis. Members of the genus *Exodontha* may be recognized by their rather large, robust form and the lack of preapical transverse grooves on the abdominal tergites. Other characters include eyes densely pilose, holoptic in males, widely separated in females; antennae with basal two segments subequal, flagellum with eight flagellomeres; palpi two-segmented; thorax quite convex, scutellum with three to four pairs

of spines; middle tibia with one small apical spur; wing with R_4 and r-m present, M_1 and M_2 petiolate to separate at discal cell, M_3 present, but abbreviated, not reaching wing margin; stigmal area elongate, narrow; abdomen broad, the first five segments large, with six and seven telescoping into the abdomen.

Exodontha is not likely to be confused with any other North American genus of Beridinae because of its large, robust size. *Allognosta* is the only other genus with a spur on the middle tibia, but it is much smaller, possesses preapical transverse grooves on the abdominal tergites, and has no spines on the scutellum. The genus *Exodontha*, as recognized here, is a genus with two species, both of which are found in the Nearctic Region. One of these is also found in northern areas of the Palaearctic Region. James (1973) synonymized *Exodontha* with *Antissa* Walker, a genus based on the type species *Clitellaria cuprea* Walker from Australia. I have examined a number of the Australian and Neotropical forms assigned to the "Antissini," and while they may well be closely related to *Exodontha*, I cannot concur with the above synonymy. The form of the antennae and male genitalia is quite different in these Southern Hemisphere forms; thus at present it is best to consider *Exodontha* generically distinct. It is apparent from the generic diagnosis that this genus is rather divergent from the other Beridinae. The lack of transverse preapical tergal grooves on the abdomen, and the reduced sixth and seventh abdominal segments are exceptional in this regard. A revision of the genera of Beridinae is needed to clarify the relationships of these genera, and such studies may well indicate that the genera related to and including *Antissa* and *Exodontha* should be removed from the subfamily. Hardy (1932) and James (1973) consider the group to be a component of the diverse subfamily Clitellariinae, and it has occasionally been accorded subfamilial rank (White, 1916; Daniels, 1978). I prefer to assign *Exodontha* to the Beridinae at present simply because it has traditionally been placed in that subfamily in recent revisions and catalogs (James, 1965; McFadden, 1967; Rozkošný, 1973) that deal with the Nearctic and Palaearctic faunas, and because its affinities have not otherwise been adequately documented.

KEY TO THE SPECIES OF *EXODONTHA*

1. Legs usually with femora and tibiae dark medially; gonostyli of males with dorsomedial process well developed, widely diverging from the main lobe (Figs. 51, 52); aedeagus subequal in length to the aedeagal valves (Fig. 49); ventral patch of spinules on aedeagal complex large (Fig. 50); western and northern in distribution ..... *dubia* (Zetterstedt)

   Legs usually wholly yellow; gonostyli of males with dorsomedial process poorly developed, hardly diverging from the main lobe (Figs. 57, 58); aedeagus shorter than the aedeagal valves (Fig. 54); ventral patch of spinules on the aedeagal complex small (Fig. 55); eastern, Appalachian distribution ..... *luteipes* (Williston)

Exodontha dubia (Zetterstedt)

Beris dubia Zetterstedt, 1838: 512.
Exodontha pedemontana Rondani, 1856: 169.
Scoliopelta grandis James, 1938: 156. NEW SYNONYMY.

Type Material. A male specimen in the Zetterstedt collection at the Entomological Museum, Zoological Institute, Lund, Sweden, is labeled as the lectotype of *Beris dubia* (by Rozkošný). The specimen is missing both third antennal segments, the left front leg beyond the trochanter, the last tarsomere of the right front leg, and has a little mold on it.

I have not examined the type of *Exodontha pedemontana* Rondani, and do not know where it is presently housed.

The holotype female of *Scoliopelta grandis* James is presently housed in the James Entomological Collection at Washington State University, Pullman, Washington. It was originally said to be in the

collection of Oregon State University (James, 1938). The holotype is missing the right antennal flagellum, the left front tarsus, the last tarsomere of the right front leg, both middle legs (which are glued to the locality label), and the right wing.

Diagnosis. This species is characterized primarily by the male genitalia, as outlined in the key. The shape of the gonostylus with its large dorsomedial process is particularly useful because it may be viewed without dissection. Females are very difficult to identify on a morphological basis; at present they may be identified most reliably by where they were collected, i.e., from the western and northern parts of the North American continent. The leg coloration is frequently but not always dark, while the legs of *E. luteipes* are nearly always wholly yellow.

Description. Male. Head black, frons and face strongly pollinose; face slightly concave toward middle, with irregular, oblique, longitudinal striations; entire head pilose, hairs of ocellar tubercle blackish, pile of eyes brownish, rest of head with pale yellowish hairs, sometimes a few darker hairs present on face; length of pile fairly uniform, about 1.5 times as long as the first antennal segment, that on lower face longer, and longest on genae where it is almost as long as the antennal flagellum; antennae 0.6 to 0.7 length of head; flagellum elongate conical, about twice as long as both basal segments combined; antennae dark brown to black, apical margin of second segment may be yellowish, inner portion of flagellum occasionally very faintly lighter; longer hairs on antennae a mixture of pale and dark; palpi black, basal segment may be brownish; proboscis brownish yellow. Thorax blackish, often with metallic greenish reflections, densely but finely punctate; humeri, postalar calli, lateral part of mesonotal suture, and sometimes extremities of scutellum brownish yellow to yellowish; pleura concolorous with mesonotum but usually without metallic reflections, sometimes brownish around sutures, the sclerites below the wing base usually brownish; almost entire thorax clothed with pale whitish yellow hairs, sometimes darkish on mesal portion of mesonotum and scutellum, averaging a little longer in length than both basal antennal segments combined; posterior part of pteropleuron and almost entire hypopleuron bare; legs dark brown except for yellowish coloration on apices of all femora, bases and extreme apices of all tibiae, and basal two-thirds of basitarsi and basal halves of tarsomeres two and three of all legs; wings light grayish brown, evenly set with microtrichia, stigma darker but not strongly contrasting with rest of wing; halter yellow, stem sometimes brownish. Abdomen dark brown to blackish, finely punctate; basal rows of pits on tergites two to five rather confused, individually indistinct; fifth tergite with fine, transverse sculpturing; pilosity mostly dark, short medially, longest laterally, sternites with appressed, short, pale yellowish pile; hypopygium yellowish brown, tenth tergite rounded posteriorly (Fig. 48); genitalia (Figs. 49–52) with ventral bridge of gonocoxites without medial process; gonostyli large, with dorsomedial process large, diverging strongly from main lobe (Figs. 51, 52); aedeagus subequal in length to the aedeagal valves, which are attenuated posteriorly (Fig. 49); spinules of aedeagal complex forming a large patch (Fig. 50). Length 7.4 to 8.8 mm.

Female. Differs from male as follows: head may be brownish; lower frons and face pollinose, sharply delimited from the finely punctate upper frons by a transverse line; width of frons at anterior ocellus 0.40 to 0.47 width of head; upper frons with a very shallow medial longitudinal depression; frontal and occipital eye margins very narrowly pollinose; pilosity of head shorter than in male, not longer than the length of the first antennal segment, pale, except darkish on eyes. Thorax with pile

shorter than that of male, wholly pale, semiappressed on mesonotum; legs may be lighter in color than in male, in the palest specimens they may be wholly yellow. Both thorax and abdomen with more extensive brown areas than found in males, occasionally almost wholly brown. Female terminalia with no distinctive specific features, essentially the same as figured for *E. luteipes* (Fig. 56). Length 7.8 to 11.3 mm.

Distribution (Map 2 shows Nearctic portion). Holarctic; ranging from Scandinavia and mountainous regions in central Europe east to Japan in the Palaearctic Region (Nartshuk and Rozkošný, 1975: 88, map) and from the Pacific Northwest east to Quebec in the Nearctic Region.

Locality Records (10 males, 10 females). CANADA: *British Columbia:* Hope Mts. (1♀); Robson (2♂, 2♀); St. Marys (1♀); Skeets Falls (1♂). *Quebec:* Mistassini Post (1♂). UNITED STATES: *Idaho:* Kootenai Co., 10 mi. N of Harrison on Lake Coeur d'Alene, 2100 ft. (1♀); Shoshone Co., Wallace (3♂, 2♀); Valley Co., 1–10 mi. S of Smith's Ferry (1♂). *Oregon:* Baker Co., Lower Goose Creek, 36 mi. SE of Union, 4000 ft. (1♂); Clatsop Co., Cannon Beach (1♀). *Washington:* Asotin Co., Fields Spring State Park (1♀); Grays Harbor Co., 2 mi. S of Queets (1♂); Whitman Co., Kamiak Butte (1♀).

Flight Period. Dates of collection range from 3 June to 12 August.

Biology. McFadden (1967) found and reared larvae of what is almost certainly this species (from Banff National Park, Alberta), which were identified as *E. luteipes*, since the identity of western specimens was not known at that time. They were found in "moist rotting wood under large boulders on a mountainside at an elevation of approximately 6000 ft." Adults occur in forested areas, but little is known of their habits. Specimens have been collected by sweeping and in Malaise traps baited with CO_2.

Remarks. The identities of the Nearctic members of this genus have been confused until now, in part due to their rarity. All specimens have been known under the name *Exodontha luteipes* (Williston), except for two female specimens that were identified as *E. grandis* (James) (the holotype and one additional specimen). It has been discovered during the course of this work that specimens from the northwestern United States and Canada were conspecific with *Exodontha dubia* (Zetterstedt), a well known but rare species previously known only from the Palaearctic Region. I have examined the Zetterstedt type which confirmed this identity.

The holotype female of *Scoliopelta grandis* James was also examined, and I have concluded that it is a junior synonym of *E. dubia.* It is unfortunate that the specimen is a female, as females are very difficult to identify reliably in this genus. The female genitalia have not proved diagnostic as they have in other Beridinae. The brownish color, the length of M_3, and the separation of M_1 and M_2 at the discal cell, all of which were characters used to characterize *E. grandis*, are variable within this species. Consequently, I feel that this taxon is best relegated to synonymy under *E. dubia* until evidence is discovered to the contrary. It should be pointed out that McFadden (1972) also suspected this synonymy.

As mentioned above, the coloration of this species is variable. It is possible that this is simply a reflection of the maturity of specimens at capture. The female genitalia are not specifically distinct; they are illustrated for *E. luteipes* only, for the sake of comparison with other genera treated in this paper. At present, females are best identified by where they were collected, but due to the rarity of both species in the genus, their distributions are incompletely known. To give some indication of the reliability of the locality records cited in this paper, I have included the sexes of the specimens examined from each locality in that section.

Exodontha luteipes (Williston)

Scoliopelta luteipes Williston, 1885: 154.

Type Material. The lectotype of *Scoliopelta luteipes* Williston is presently housed in the Snow Entomological Museum at the University of Kansas, Lawrence, Kansas. The male specimen is in perfect condition. The lectotype was designated by McFadden (1972; the second original label reads "Aug.," not "A. Fig." as indicated by McFadden).

Diagnosis. Male genitalic characters outlined in the key are the only reliable characters useful for determining members of this species. The small dorsomedial process of the gonostylus may be viewed without dissection. Female specimens may be identified most reliably by their collection sites; the species has an Appalachian distribution. A character of limited usefulness is the leg coloration. The legs are wholly pale in all specimens examined except one, whereas they are frequently darker in *E. dubia,* often having the femora and tibiae with extensive dark brown coloration.

Description. Male. Similar to *E. dubia,* but differing as follows: head with eye pilosity sparser, subequal in length to the first antennal segment; antennae with basal two segments brownish, yellowish at apex of second, inner portions of flagellomeres three to five with distinct light brownish area. Thorax with mesonotum with metallic reflections rather more bronzy; lateral areas paler, brownish yellow, irregularly more extensive than in *E. dubia,* extending along lateral margins and often onto scutellum; pleura brownish, with the areas which are brownish in *E. dubia* quite yellowish, including sclerites below wing base; pile of thorax more golden yellow; legs wholly orangish yellow, femora may be faintly darker. Abdomen brownish, sometimes with an almost purplish cast; basal rows of pits on tergites two to five with individual pits distinct; pilosity pale, golden colored; genitalia (Figs. 53–55, 57–58) with gonostyli only slightly bilobed, the dorsomedial process reduced (Figs. 57, 58); aedeagus shorter than aedeagal valves, which are truncate apically (Fig. 54); spinules on ventral surface of aedeagal complex less extensive (Fig. 55); tenth tergite truncate posteriorly (Fig. 53). Length 7.1 to 8.1 mm.

Female. Extremely similar to *E. dubia*; frons 0.37 to 0.47 width of head; coloration more brownish than in males, especially the thorax; legs as in male, except in one specimen they are similar in coloration to those of *E. dubia* (see below). Genitalia (Fig. 56) very similar to those of *E. dubia.* Length 7.0 to 9.3 mm.

Distribution (Map 2). Known from the Appalachian region of eastern North America, from Vermont and New Hampshire south to North Carolina.

Locality Records. (14 males, 8 females). UNITED STATES: *Massachusetts:* Hampden Co., Chester (7♂, 1♀). *New Hampshire:* White Mts. (2♂, 1♀); Grafton Co., Franconia (1♂). *New York:* Essex Co., Upper Ausable (1♂); Orange Co., Bear Mtn. (1♀); Schuyler Co., Texas Hollow (1♀). *North Carolina:* Macon Co., Highlands (Horse Cove) (1♂); Transylvania Co., Pisgah Forest, Looking Glass Park (1♂, 5♀). *Vermont:* Camel's Hump (1♀); Rutland Co., Rutland (2♀); Windsor Co., Woodstock (1♂).

Flight Period. Specimens have been collected from 19 July to 30 August.

Biology. Nothing is known about this species, either for the immature stages or adults.

Remarks. The name *Exodontha luteipes* has long been used for nearly all North American specimens of this genus. Examination of the lectotype of this species has confirmed the application of this name to this taxon, which was found to be distinct from specimens from Canada and the western United States, which are properly assigned to *E. dubia* for the first time in this paper. *Exodontha luteipes* is apparently restricted to the Appalachian region, and is not known to be

sympatric with *E. dubia*. One specimen, a female from Chester, Massachusetts, in the collection of the Museum of Comparative Zoology, has leg coloration that is similar to that found in *E. dubia*, however, and it may be that species. It would appear that if the two species were to have overlapping distributions, it would most likely be in the northern part of the range of *E. luteipes*. Thus a Massachusetts locality for *E. dubia* seems at least possible. Specimens of both species are quite scarce, and a full understanding of their distributions and identities must await the collection of more material, especially males.

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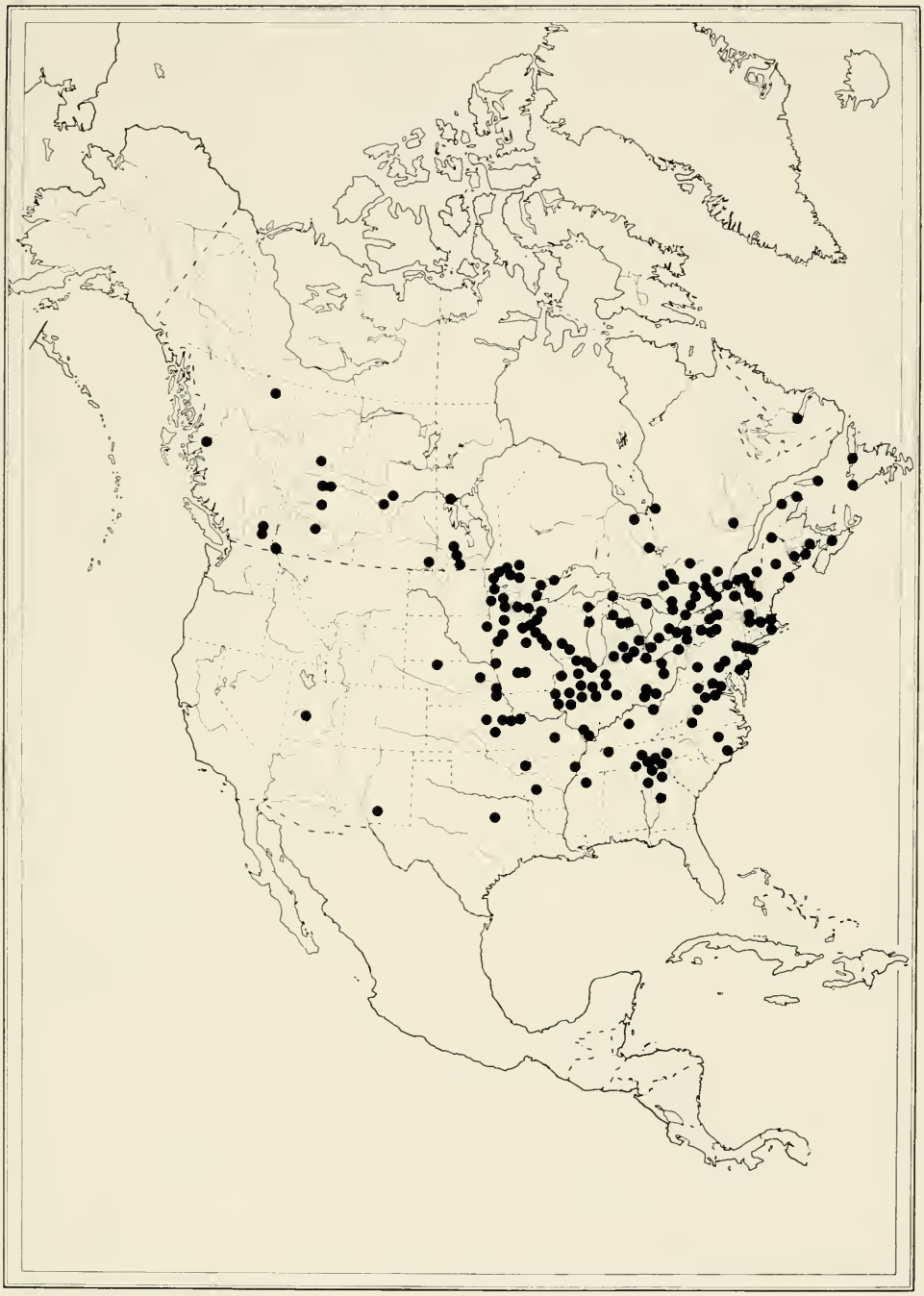
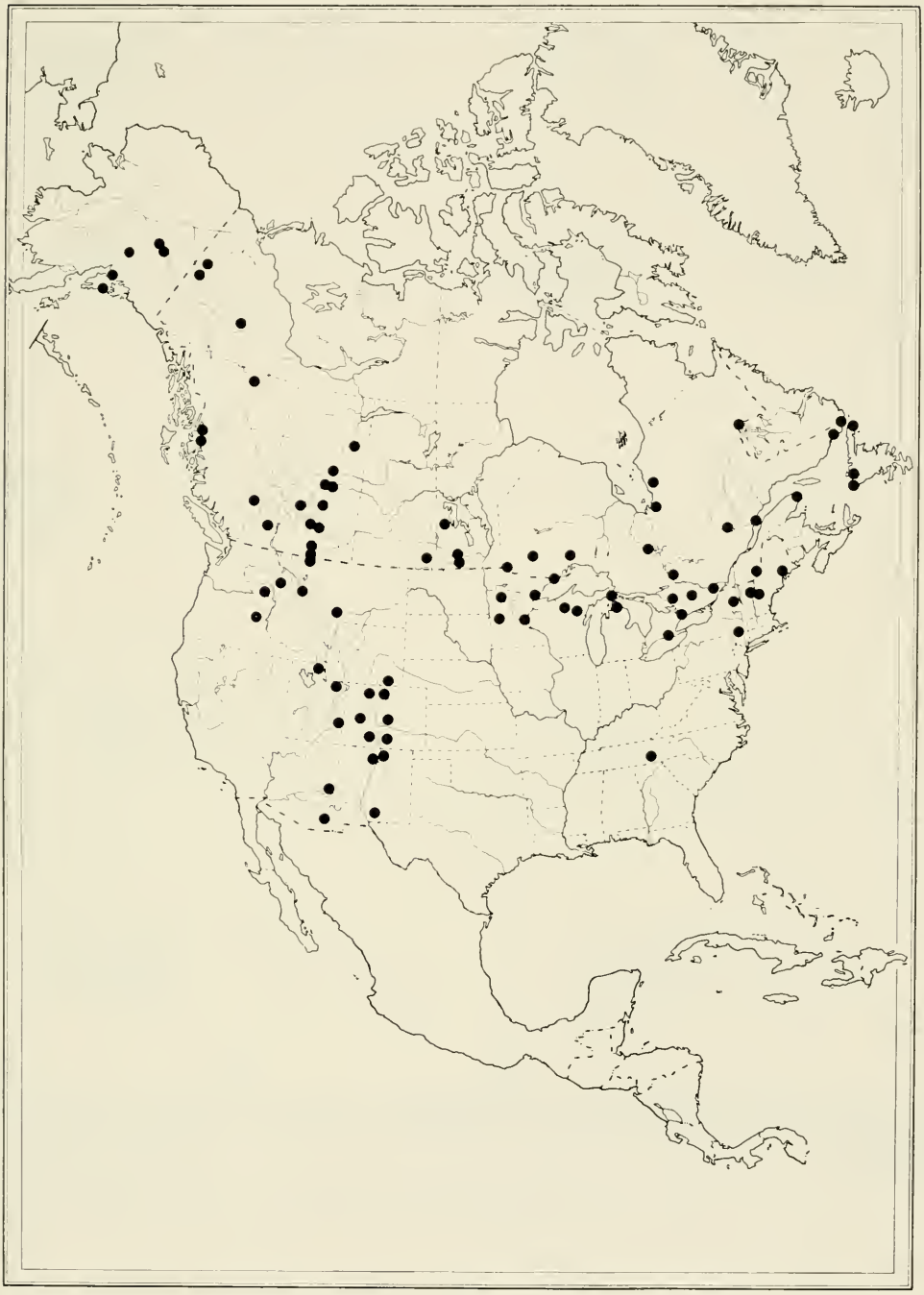


Map 1. Distribution of *Actina viridis* (Say).

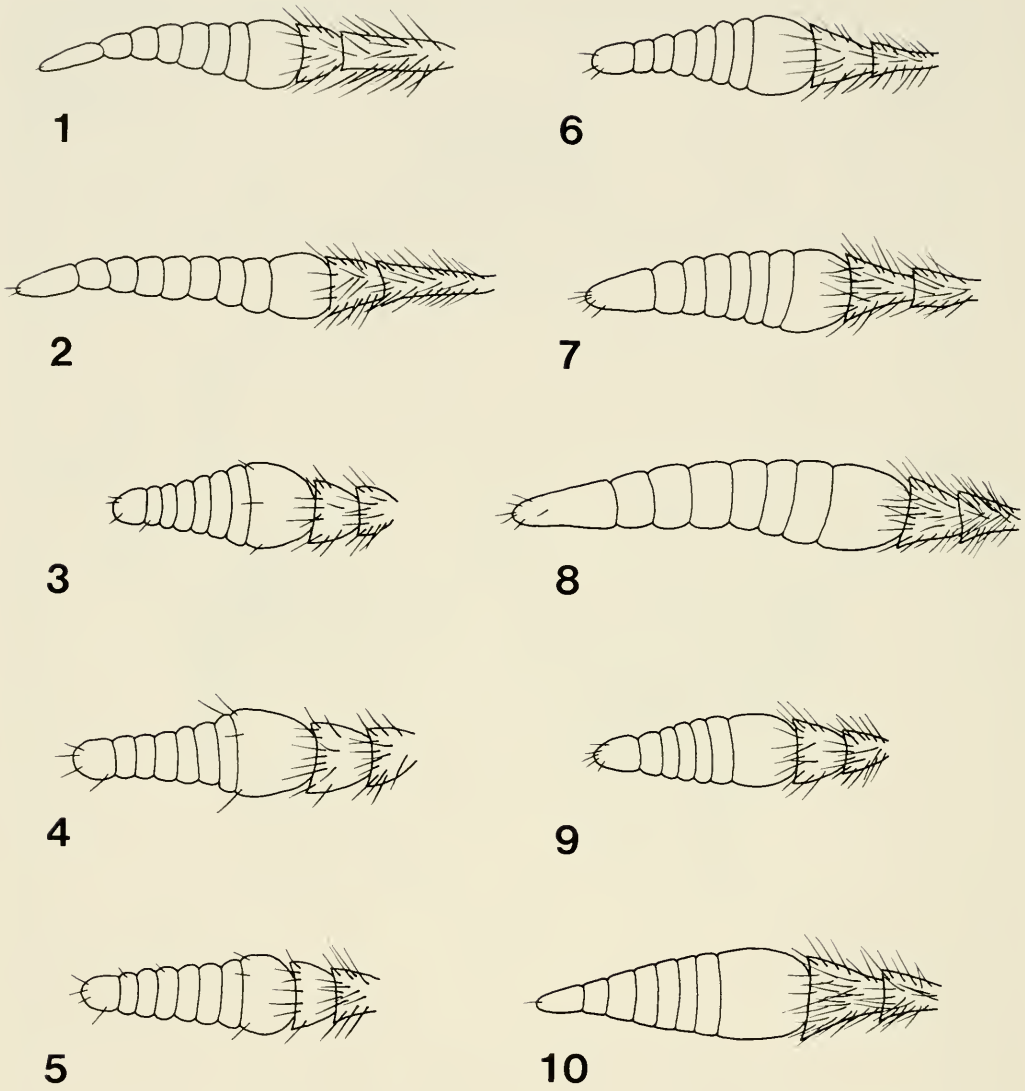
Map 2. Distributions of Beridinae: ●, *Allognosta brevicornis* Johnson; ▲, *Exodontha luteipes* (Williston); ■, Nearctic distribution of *Exodontha dubia* (Zetterstedt).

Map 3. Distribution of *Allognosta obscuriventris* (Loew).

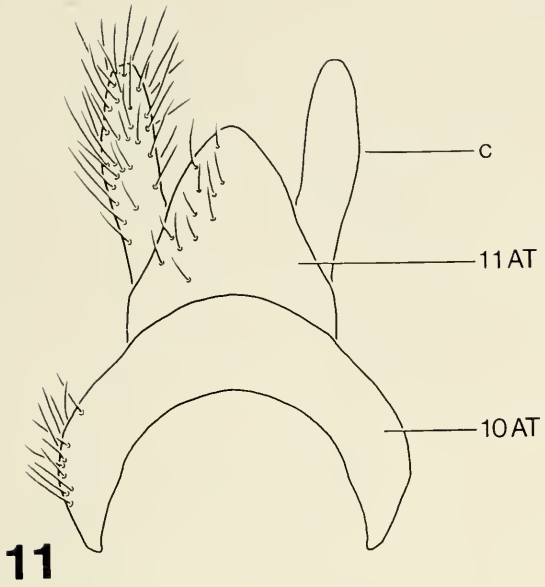
Map 4. Distributions of Beridinae: ●, *Allognosta fuscitarsis* (Say); ▲, Nearctic distribution of *Beris strobli* Dušek and Rozkošný; ■, *Beris luteipes* Johnson.



Map 5. Nearctic distribution of *Beris fuscipes* Meigen.



Figures 1–10. Antennae of Beridinae. 1. *Actina viridis* (Say), male. 2. *Actina viridis* (Say), female. 3. *Allognosta brevicornis* Johnson. 4. *Allognosta fuscitarsis* (Say). 5. *Allognosta obscuriventris* (Loew). 6. *Beris fuscipes* Meigen. 7. *Beris luteipes* Johnson, male. 8. *Beris luteipes* Johnson, female. 9. *Beris strobli* Dušek and Rozkošný. 10. *Exodontha dubia* (Zetterstedt).



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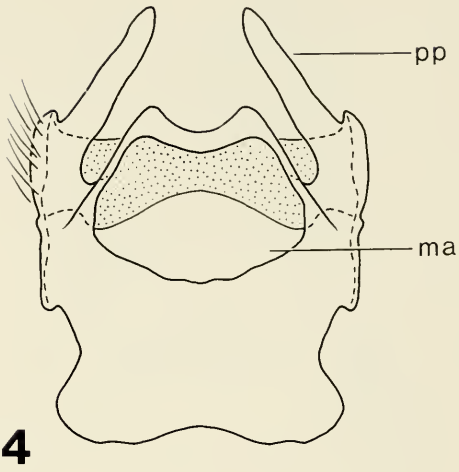

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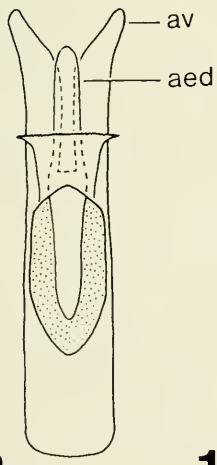

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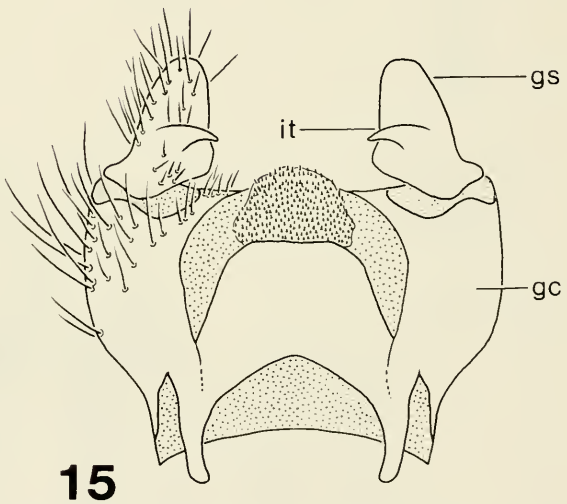

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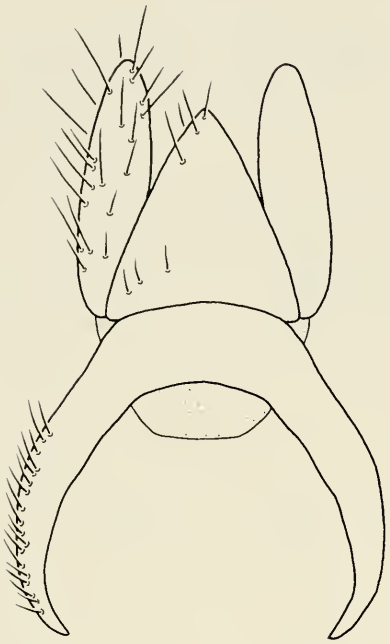
Figures 11–15. Male and female genitalia of *Actina viridis* (Say). 11. male post-genital segments, dorsal view. 12. male aedeagal complex, dorsal view. 13. male aedeagal complex, lateral view. 14. female genital furca, ventral view. 15. male genital capsule, dorsal view.

Abbreviations: aed, aedeagus; AT, abdominal tergite; av, aedeagal valve; c, cercus; gc, gonocoxites; gs, gonostylus; it, internal tooth; ma, median aperture of genital furca; pp, posterolateral process.



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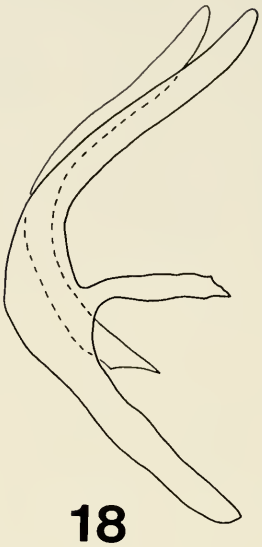

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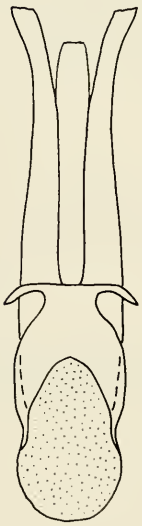

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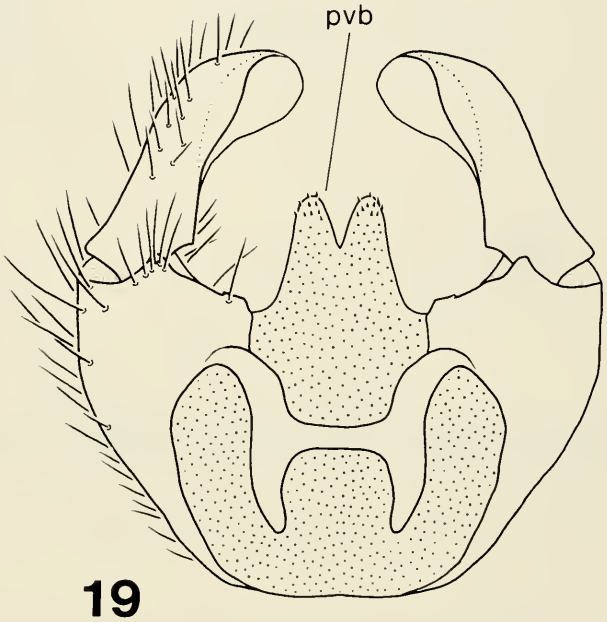

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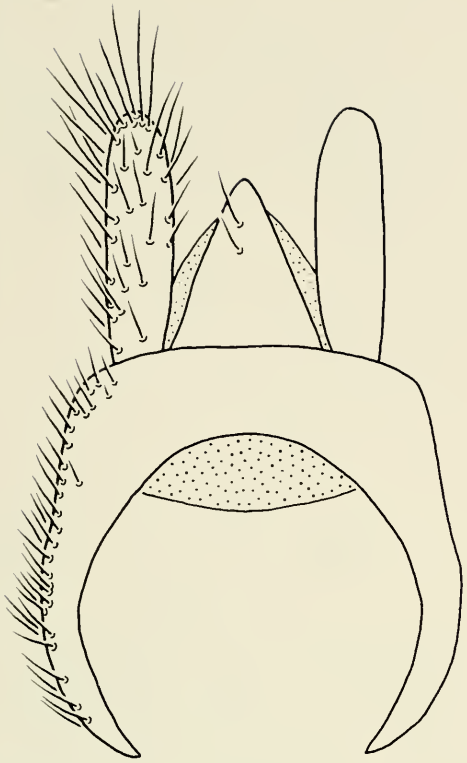
Figures 16–19. Male genitalia of *Allognosta brevicornis* Johnson. 16. post-genital segments, dorsal view. 17. aedeagal complex, dorsal view. 18. aedeagal complex, lateral view. 19. genital capsule, dorsal view.

Abbreviation: pvb, process of ventral bridge of gonocoxites.



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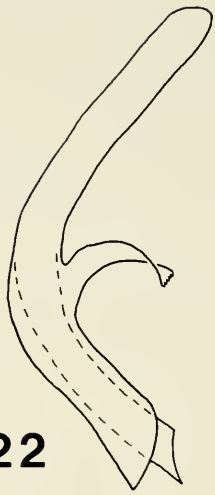

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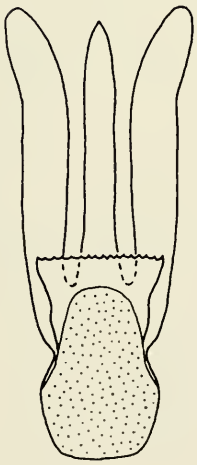

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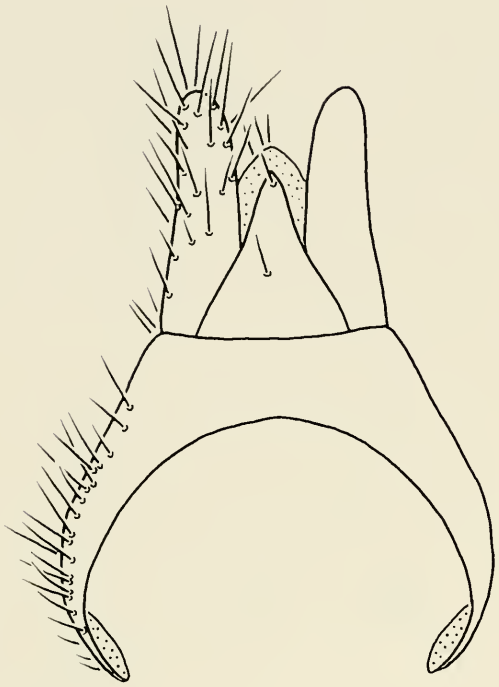
Figures 20–23. Male genitalia of *Allognosta fuscitarsis* (Say). 20. post-genital segments, dorsal view. 21. aedeagal complex, dorsal view. 22. aedeagal complex, lateral view. 23. genital capsule, dorsal view.



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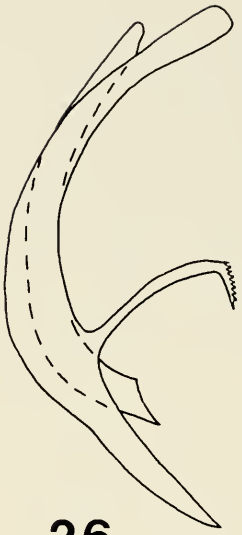

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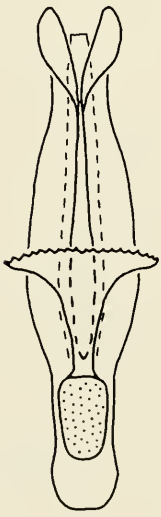

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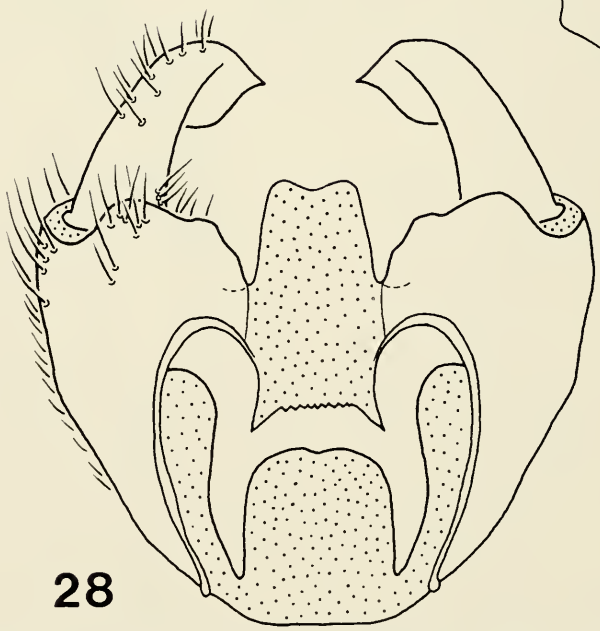

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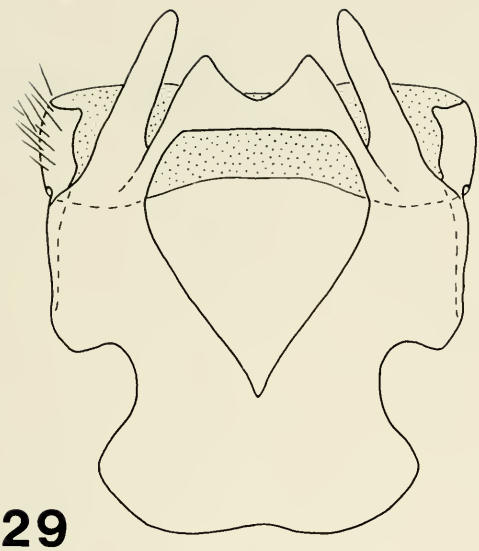
Figures 24–28. Male genitalia of *Allognosta obscuriventris* (Loew). 24. post-genital segments, dorsal view. 25. aedeagal complex, dorsal view. 26. aedeagal complex, lateral view. 27. gonostylus, variant, same view as for genital capsule. 28. genital capsule, dorsal view.



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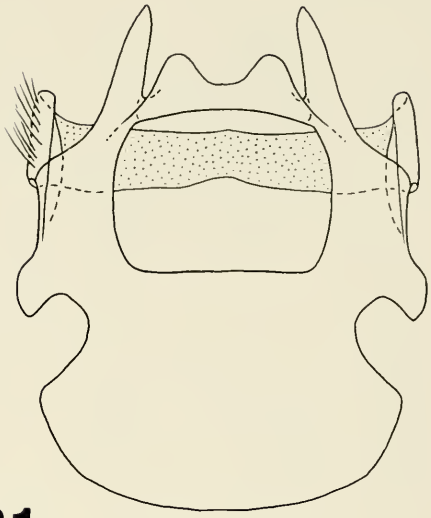

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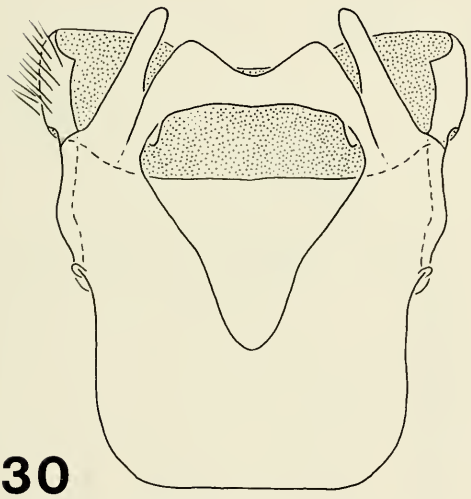

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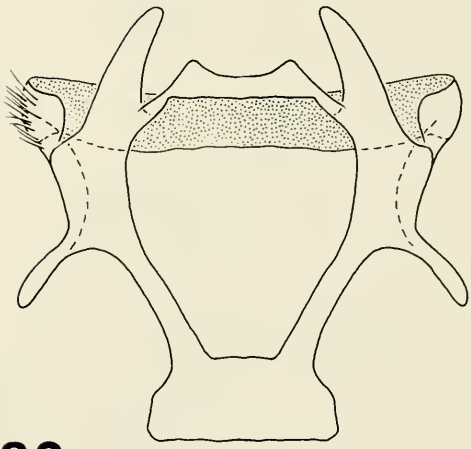

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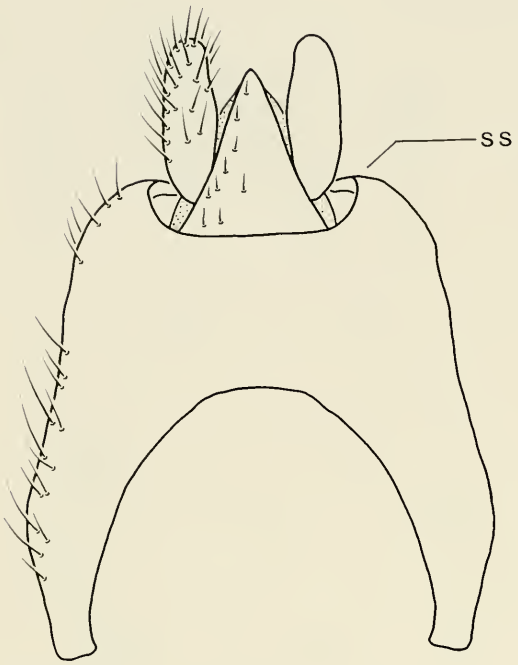
Figures 29–32. Female genital furcae of *Allognosta* spp., ventral views. 29. *A. obscuriventris* (Loew). 30. *A. obscuriventris* (Loew), variant. 31. *A. fuscitarsis* (Say). 32. *A. brevicornis* Johnson.



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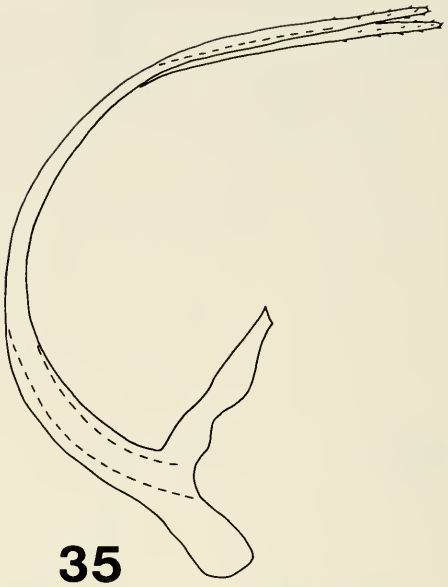

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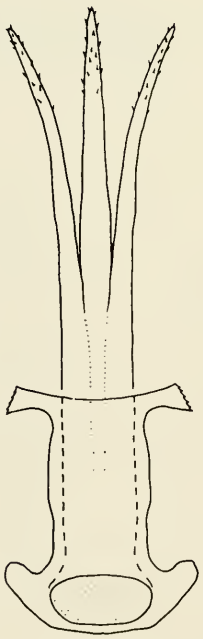

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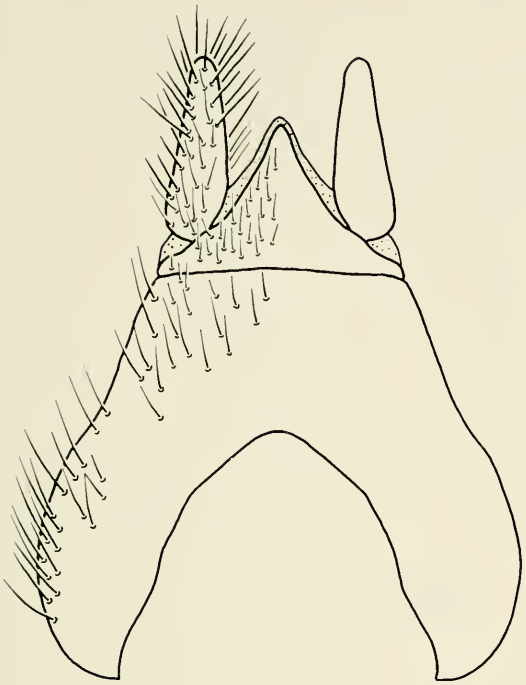
Figures 33–36. Male genitalia of *Beris fuscipes* Meigen. 33. post-genital segments, dorsal view. 34. aedeagal complex, dorsal view. 35. aedeagal complex, lateral view. 36. genital capsule, dorsal view.

Abbreviation: ss, surstylus.



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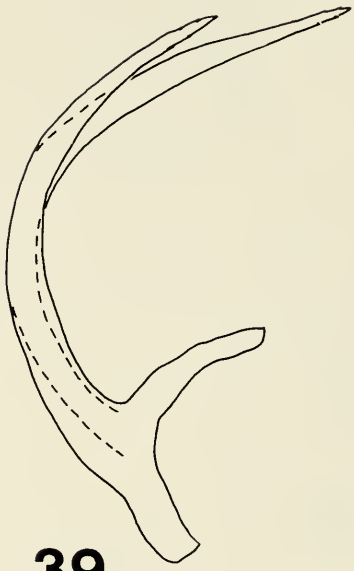

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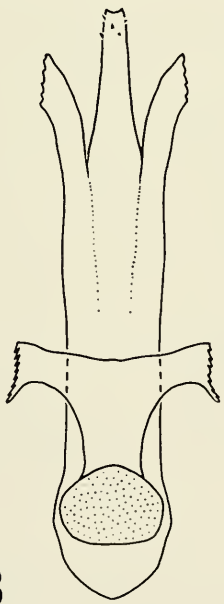

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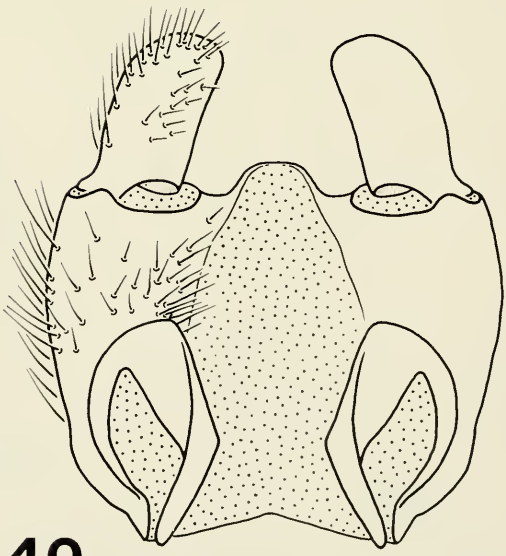

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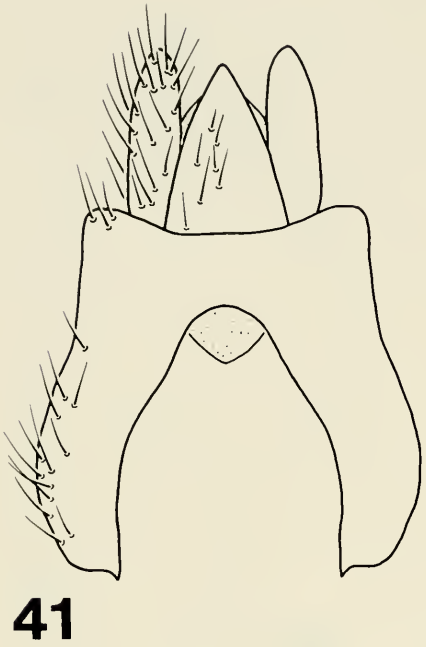
Figures 37–40. Male genitalia of *Beris luteipes* Johnson. 37. post-genital segments, dorsal view. 38. aedeagal complex, dorsal view. 39. aedeagal complex, lateral view. 40. genital capsule, dorsal view.



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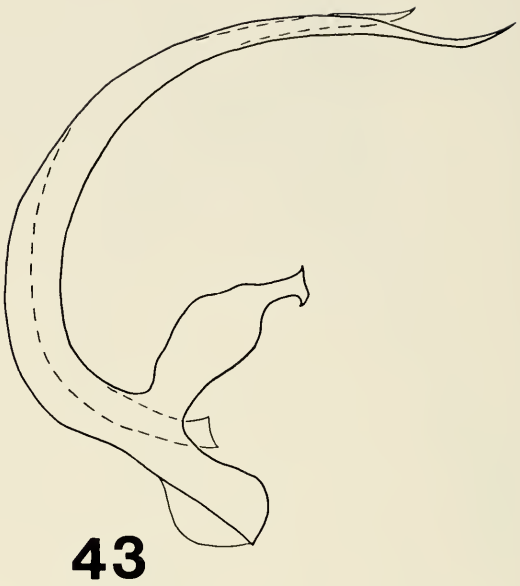

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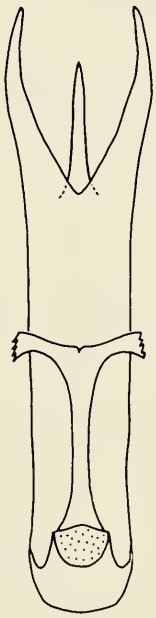

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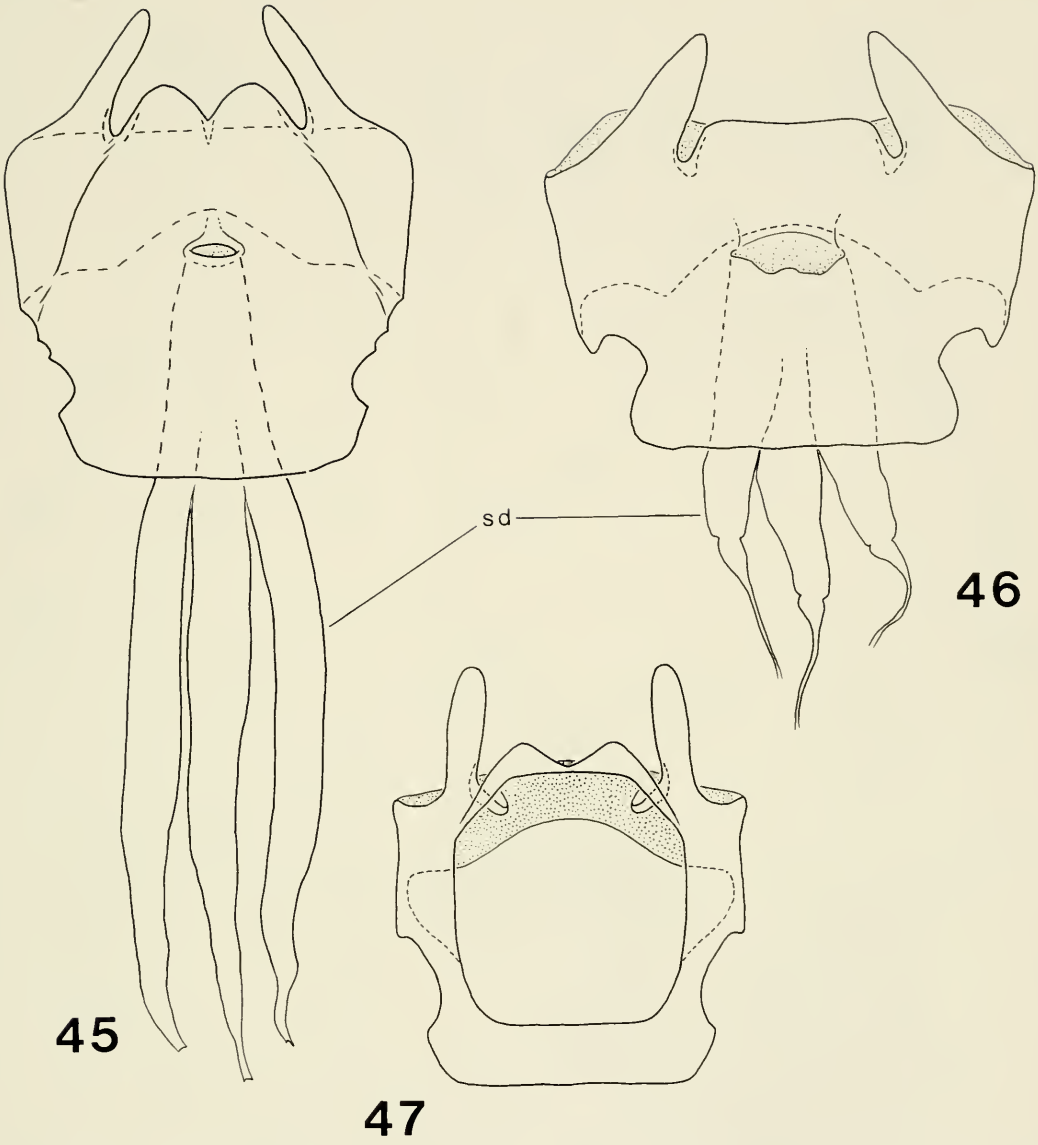
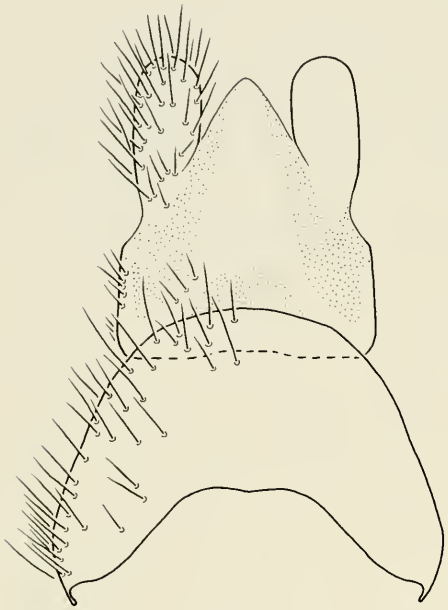
Figures 41–44. Male genitalia of *Beris strobli* Dušek and Rozkošný. 41. post-genital segments, dorsal view. 42. aedeagal complex, dorsal view. 43. aedeagal complex, lateral view. 44. genital capsule, dorsal view.



Figures 45–47. Female genital furcae of *Beris* spp., ventral views. 45. *B. fuscipes* Meigen. 46. *B. luteipes* Johnson. 47. *B. strobli* Dušek and Rozkošný.

Abbreviation: sd, spermathecal duct.



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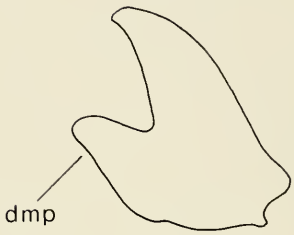

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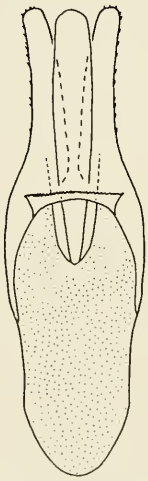

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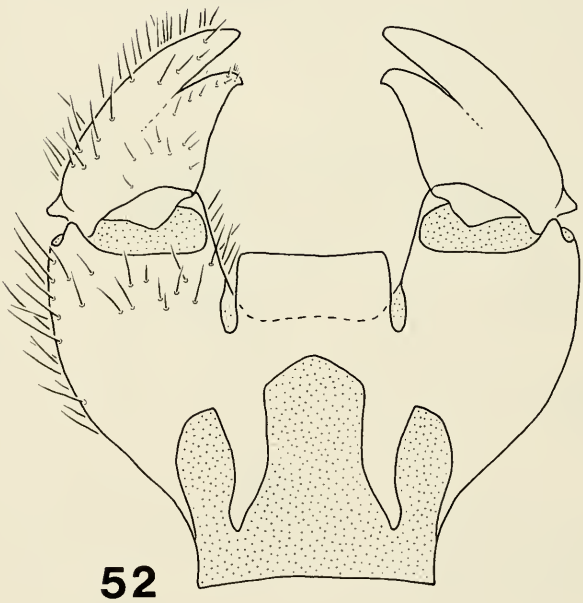

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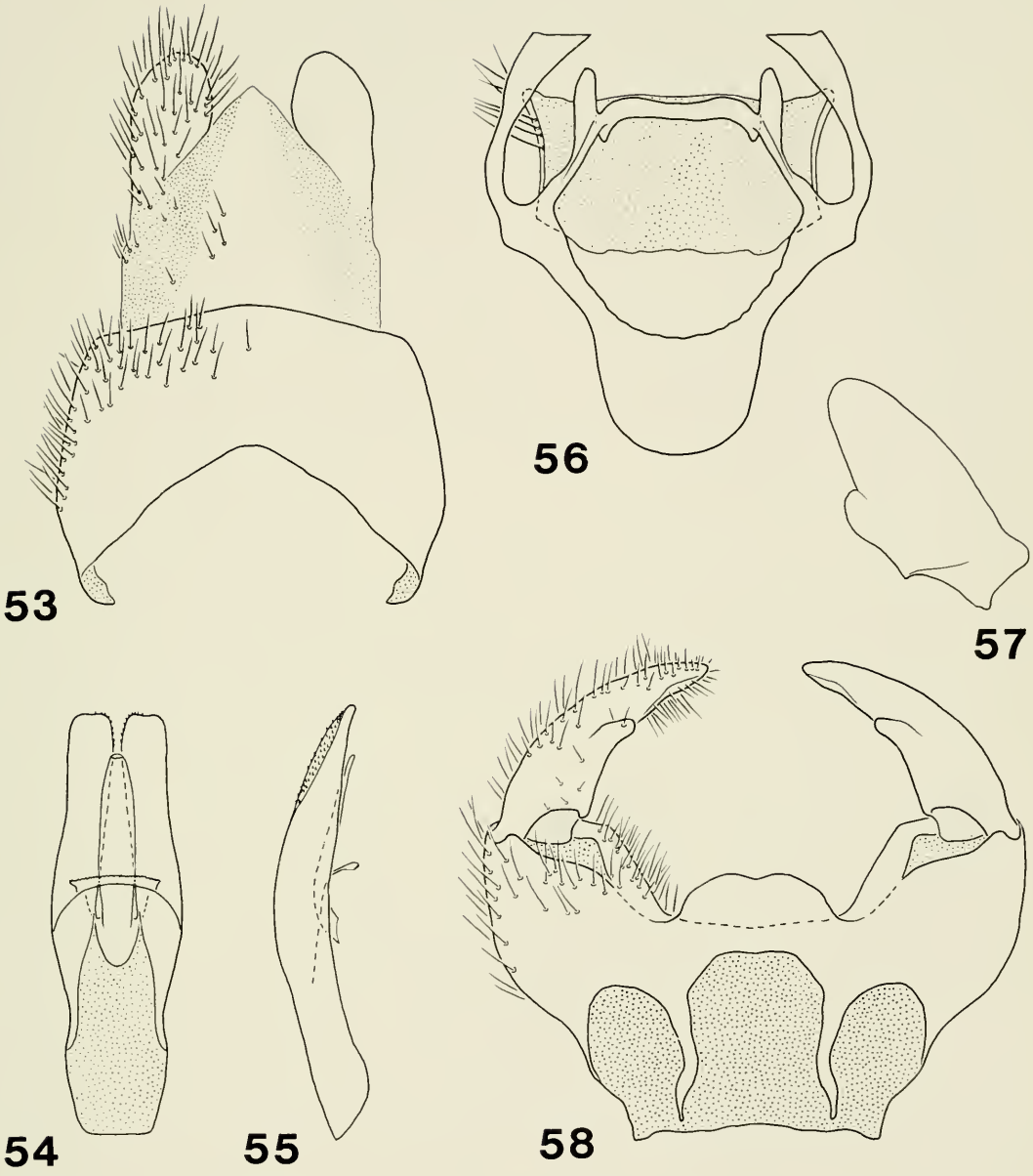
Abbreviation: dmp, dorsomedial process.



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Rodents from the Deseadan Oligocene of Bolivia and the Relationships of the Caviomorpha

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RODENTS FROM THE DESEADAN OLIGOCENE OF BOLIVIA AND THE RELATIONSHIPS OF THE CAVIOMORPHA

BRYAN PATTERSON[1] and ALBERT E. WOOD[2]

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ABSTRACT. The extensive Princeton collections of fossil caviomorph rodents from the early Oligocene Deseadan of Bolivia are described. Much new information is reported concerning the teeth and skulls of *Sallamys pascuali, Incamys bolivianus,* and *Branisamys luribayensis,* only one species of each genus being recognized. These are referred to the Echimyidae, Dasyproctidae, and Dinomyidae, respectively. An octodontid, *Migraveramus beatus,* n. gen., n. sp., is described. Lavocat's description of *Cephalomys bolivianus* is briefly reviewed. Two undescribed dasyproctid genera are reported. *Luribayomys masticator* and *Palmiramys waltheri* (the latter from Uruguay) are considered to be *nomina vana.*

The two theories for the origin of the caviomorphs are reviewed. The first states that they are descended from African thryonomyoids that crossed the South Atlantic as waif migrants. The second derives them from Middle American franimorph ancestors that reached South America, also as waif migrants, either directly or through the Antilles.

Eocene hystricognathous rodents have so far been reported only from North America. There is good negative evidence that none reached Europe, but they presumably did reach Asia when that continent was connected with North America, both early and late in the Eocene.

The early Oligocene South American and Egyptian rodent faunas are compared and contrasted, and compared with localized collections of Recent rodents from northeastern Brazil. The differences between and general composition of the various Deseadan local faunas are comparable to those between individual Recent sites. The African Oligocene rodents seem not so diversified as are the modern Australian Pseudomyinae. These latter have achieved their current diversity in about 4.5 m.y. It is proposed that rodents reached Africa no more than this length of time before the lowest fossil levels of the Fayum. The Deseadan rodents are as diversified as are those of the early Miocene of East Africa, and had presumably been in South America about as long before the Deseadan as the thryonomyoids had been in Africa before the early Miocene. This would place the arrival of rodents in South America in the middle Eocene.

The Eocene geography of southern Central America and the Antilles was such that migration of ancestral caviomorphs from Middle to South America, either directly or through the Antilles, would have been entirely possible. It is probable that there was a single invading stock, although there is evidence supporting a distinct origin for the Erethizontidae.

Parasitic nematodes have been cited as supporting a thryonomyoid ancestry of the Caviomorpha. The evidence is reviewed, and it is concluded that there is no valid evidence to support such a hypothesis. In every case of supposed close relationship of nematodes parasitic on Old and New World forms, there is reason to question the validity of the conclusions.

The morphologic evidence used by Lavocat to support the derivation of the Oligocene South American Caviomorpha from the contemporaneous Thryonomyoidea of Africa is reviewed. It is concluded that, although there are many similarities between the Old and New World forms, the evidence indicates that the African forms could (morphologically) have been derived from the South American ones, but that the reverse is structurally impossible. It is concluded that both groups were derived, independently, from Holarctic Eocene members of the Infraorder Franimorpha. The lice and fleas of hystricognaths support the concept that the Hystricognathi are a natural group, but do not allow one to choose between the two hypotheses for the origin of the caviomorphs.

The suprafamilial classification of all hystricognath rodents (Suborder Hystricognathi) is reviewed. Among the Caviomorpha, we now follow a growing consensus that the Families Dasyproctidae, Dinomyidae and Cuniculidae should be transferred from the Superfamily Chinchilloidea to the Superfamily Cavioidea. These families form a group (Series B) distinct from the Families Eocardiidae, Caviidae and Hydrochoeridae (Series A). The Echimyidae are an even more complex group than previously believed, the genus *Chaetomys* (Subfamily Chaetomyinae) being transferred from the Erethizontidae to the Echimyidae. The two subfamilies Capromyinae and Plagiodontinae, formerly included by us in the Family Capromyidae, are likewise here transferred to the Echimyidae. This combines all caviomorphs that ever retain dm_4^4 throughout life in the Family Echimyidae.

The Superfamily Erethizontoidea is retained in the Caviomorpha, in spite of evidence that it is quite distinct from the rest of the infraorder. It was presumably an early offshoot of the basal stock of the Caviomorpha.

The Family Neoepiblemidae is added to the Chinchilloidea as a second family. The Family Heptaxodontidae is left *incertae sedis* as to superfamily.

The Eocene to Oligocene Infraorder Franimorpha, including the Families Reithroparamyidae (new rank), Protoptychidae, Cylindrodontidae, and two genera *incertae sedis* as to family, is considered to have been ancestral to all other hystricognaths. In the Old World, Eocene franimorphs are still unknown, the Chapattimyidae of Pakistan and India being shown to be ctenodactyloids.

The Tsaganomyidae (new rank) of north Asia are considered to be cylindrodont descendants, as are also the Bathyergidae. The two families differ from the cylindrodonts in being fully hystricognathous, and are united in the Superfamily Bathyergoidea. They are both fundamentally protrogomorphous.

No evidence is found for or against deriving the Thryonomyoidea from the Hystricidae. If the two

are united at the infraordinal level, the infraorder should be called Hystricomorpha rather than Phiomorpha because of the long priority and general recognition of that term.

Three families of Thryonomyoidea are recognized: Thryonomyidae, Petromuridae and Myophiomyidae. Stromer's genus *Neosciuromys*, placed in synonymy by Lavocat, is re-established.

INTRODUCTION

The Tertiary vertebrates of Bolivia are poorly known. Simpson (1940), in his summary of reported extra-Argentinian Tertiary mammals of South America, could cite only three Bolivian records, all of uncertain age: a tooth referred, perhaps incorrectly, to *Nesodon*; parts of an armadillo, the type of *Dasyptodon atavus* Castellanos; and a jaw fragment of a haplodontheriine toxodontid, the type of *Pachynodon validus* Burmeister. Discoveries of Deseadan faunas in the Cordillera Oriental of Bolivia, not far from La Paz, are therefore of the greatest interest.

The first find was made in the Salla-Luribay Basin, Provincia Loaza, Departamento La Paz, by G. Bejarano in 1962. Dr. L. Braniša began field work there in 1964. With encouragement from the late Professor Glenn L. Jepsen, he undertook intensive work in this and other localities of younger ages for Princeton University. Field, preparational, and other expenses connected with the acquisition by Princeton of the materials brought together by Braniša during 1964–1966 were met by a generous bequest from the late Gordon Barbour, a long-time friend and benefactor of the University, for the express purpose of furthering vertebrate paleontological work in Bolivia. As a result, Princeton possesses an excellent collection of Deseadan mammals from Salla-Luribay. The discovery was announced by Baird *et al.* (1966). From 1965 to 1972 Hoffstetter visited this area and made collections (Hoffstetter, 1968, 1976), and Hartenberger and Villarroel have worked at the locality since then. More recently there have been other expeditions in the area.

At Salla-Luribay, which is some 90 km SE of La Paz, about 450 m of Tertiary continental sediments rest unconformably upon folded Devonian rocks. The lower part of the Tertiary sequence consists of chocolate colored sandstone and conglomerate beds; the upper of well stratified, red and reddish-brown clays and silts with four calcareous beds distributed through the sequence (Hoffstetter, 1976: 4, 6). The lower portion was named the Luribay Conglomerate (Ahlfeld and Braniša, 1960: 132) and the higher the Estratos de Salla, or Salla Beds (Evernden *et al.*, 1966). The vertebrate remains occur in the lower part of the Estratos de Salla, the upper part of that unit and the underlying Luribay Conglomerate apparently being unfossiliferous (Hoffstetter, 1968; a notoungulate skull possibly from the conglomerate has been mentioned by Hoffstetter, 1976: 8). The thickness of the fossil bearing portion of the Salla has not been reported, although Hoffstetter (1976: 8) stated that the fossils are found "depuis la base jusqu'au 3ème niveau calcaire . . . ." We tried to measure the thickness of the fossiliferous zone from the geologic section given by Hoffstetter (1976: Fig. 3), but it would appear that the section is not to scale since, in the figure, the 300 m thick Salla Beds measure 9.5 cm, and the 150 m thick Luribay Conglomerates measure 6 cm. Hoffstetter did not state whether the section represents the maximum thickness of the formation. If it does not, and if the Salla and the underlying Luribay Conglomerate are to scale in the figure, the fossiliferous portion would be about 150 m thick. Ahlfeld and Braniša (1960: 137) note a resemblance between this sequence and the Tertiary Chacarilla Formation of the Altiplano.

Subsequent to the Salla-Luribay discovery, a second, much less extensive and less fossiliferous locality was found at Lacayani, 50 km NW of Luribay and 30 km SE of La Paz (Hoffstetter *et al.*, 1971). The Tertiary deposits there are uncon-

formable upon folded late Cretaceous and Devonian rocks, and are "some tens of meters" in thickness. The lower portion consists of alternating clays, sandstones and yellowish brown conglomerates. This is separated by a 50 cm thick cinerite from the upper, reddish clays, which contain the mammalian remains.

Rodents occur at both localities. Hoffstetter and Lavocat (1970) very briefly described three new genera from Salla: *Sallamys*, *Incamys*, and *Branisamys*. From Lacayani, Hoffstetter *et al.* (1971) have listed *Scotamys*, a genus known from Patagonia, and an eocardiid. Hartenberger (1975), listing these, has also mentioned "Octodontoidea nov. gen. 1 and 2" from Salla, and described *Villarroelomys*, also from this locality, which we believe (p. 444) to be referable to *Branisamys*. He has further recorded, again from Salla, a species of *Cephalomys*, another genus known from Patagonia. Lavocat (1976) described *Sallamys*, *Branisamys* and *Incamys* in detail, concluded that the type of *Villarroelomys* probably was dm_4 of *Branisamys* (a conclusion that we had already reached), described a second species of *Incamys*, a new species of *Cephalomys* (*C. bolivianus*) and *Luribayomys*, a new genus that he left *incertae sedis*. He was vague (1976: 59) as to whether Hartenberger's *Cephalomys* was or was not the same as *C. bolivianus*. The Princeton collection contains the jaw of a new octodontid genus, additional material of *Sallamys*, extensive and excellent material of *Incamys*, and better material of *Branisamys* than was available to Hoffstetter and Lavocat (1970) or to Lavocat (1976). These specimens are described in detail below.

There can be no doubt as to the Provincial (or Land Mammal) Age of these Bolivian faunas; each contains mammalian species inseparable from Patagonian Deseadan ones or assignable to Patagonian Deseadan genera. The two differ from each other and from Patagonian local faunas—as these latter do among themselves—regarding presence, absence or differing abundances of various faunal elements. It is not at all surprising to encounter such differences between the Bolivian and the Patagonian faunas, separated as they are by nearly 30° of latitude, but it is rather remarkable that all Deseadan local faunas, whether Bolivian or Patagonian and regardless of degree of geographic proximity, should differ to the extent that they do. The rodents, Table 8 (p. 461), are no exception. Each of the better known local faunas—Cabeza Blanca, La Flecha, Salla—contains one species that is predominant numerically and one or two that are moderately common, whereas the rest are represented only by one or two specimens. In no case is the predominant species the same in more than one locality. The question is: are these differences due primarily to age or primarily to the sampling of different ecologies?

Both views have been advanced. Hartenberger (1975) has tentatively suggested, as a working hypothesis, that Rinconada de los Lopez (Scarritt Pocket) is the earliest local fauna, Salla intermediate, and La Flecha and Cabeza Blanca the latest. This was based on the primitive nature of *Platypittamys*, on the presence of a species in the Salla local fauna (his Octodontoidea nov. gen. 1) that "on dental characters could be considered a descendant of *Platypittamys*," and on the Salla species of *Cephalomys*, stated to be small and more primitive than those occurring at Cabeza Blanca and La Flecha. Wood (1949) had previously considered Rinconada de los Lopez as being earlier than the others, also on the basis of *Platypittamys*. The alternative, ecological hypothesis is based on the local faunas as wholes. In no instance (with the possible exception of Hartenberger's octodont) is it demonstrated that a species in one local fauna is ancestral to a species in another (Wood and Patterson, 1959: 300). As Hoffstetter *et al.* (1971) have put it: ". . . les faunes . . . appartiennent au Dé-

séadien . . . sans qu'on puisse exclure la possibilité de légers décalages chronologiques, de toute façon minimes."

In agreement with these authors, we doubt that anyone would be prepared to assert that all Deseadan local faunas were exactly synchronous. Granting this, were the differences in age between them minimal in the geological sense or sufficiently long to permit evolution to or toward the species level? Support for the latter possibility must, it would seem, come from the rodents since other faunal elements do not, so far as known, favor it. The most suggestive evidence, as yet undocumented, is of course provided by Hartenberger's remark that his Salla Octodontoidea gen. nov. 1 could be descended from *Platypittamys* (a claim he has not made concerning the relationships of the *Cephalomys* present at Salla to those occurring at La Flecha and Cabeza Blanca). It is possible, however, for more primitive and more advanced, yet closely related, species to coexist in the same local fauna. *Deseadomys loomisi*, type and only known specimen from Cabeza Blanca, is larger and more advanced as regards metalophid reduction than *D. arambourgi*, type from La Flecha. If knowledge rested there it could very plausibly be argued that the latter was ancestral to the former, but negating this possibility is a specimen from Cabeza Blanca that can be referred with confidence to *D. arambourgi* (Wood and Patterson, 1959: 305). As a minor item of evidence suggesting a close approximation in time between Cabeza Blanca and Salla, we may point to the presence at the former of an isolated P^4 that we are unable to distinguish from corresponding teeth of *Incamys bolivianus*, the commonest rodent at Salla (see Table 8 and p. 429).

On the age difference side of the argument, it seems probable that the Deseadan rodents, not yet fully beyond the first flush of their initial adaptive radiation but nonetheless the most abundant group of Deseadan fossils, were evolving rapidly (more so than other faunal elements whose ancestors had been in South America for millions of years before the rodents arrived there) and should therefore be the best indicators of temporal differences within that Age. This may indeed be so, but the documentation of it is not yet satisfactory. However, the upper premolars are three-crested in all or nearly all (see below, p. 495) of the Patagonian genera in which they are known, and four- or five-crested in the ones from Salla. We believe the three-crested pattern to be the primitive one. This suggests, to Wood at least, that the Salla deposits may be later than those in Patagonia. We are open minded as regards the two hypotheses, although we must confess to differing preferences: Patterson, in agreement with Hoffstetter (1976: 11–12), inclining toward ecological differences; Wood toward age ones. (The composition of Deseadan rodent faunas is further discussed below, pp. 460–471.)

As concerns the age of the Deseadan as a unit, welcome new evidence is at hand. Marshall *et al.* (1977) have reported that a basalt above Deseadan sediments at Pico Truncado has an age of 33.6 ± .4 m.y.b.p., and another, at Cerro Blanco, apparently directly conformable upon Deseadan sediments, one of 35.4 ± .4 m.y.b.p. These authors report that the basalts record a period of volcanic activity "around 34–35 mybp," and this "is tentatively accepted as an approximate terminal date for known Deseadan." They regard the 33.6 m.y.b.p. date as being a little post-Deseadan. It is gratifying to see the previous consensus as to early Oligocene age confirmed by the new evidence; our suggestion (1959: 388) that the Deseadan was early but not earliest Oligocene may not have been too wide of the mark. How long the Age may have lasted remains uncertain. We utilize the earlier Tertiary epoch boundaries of Berggren and Van Couvering (1974: Fig.

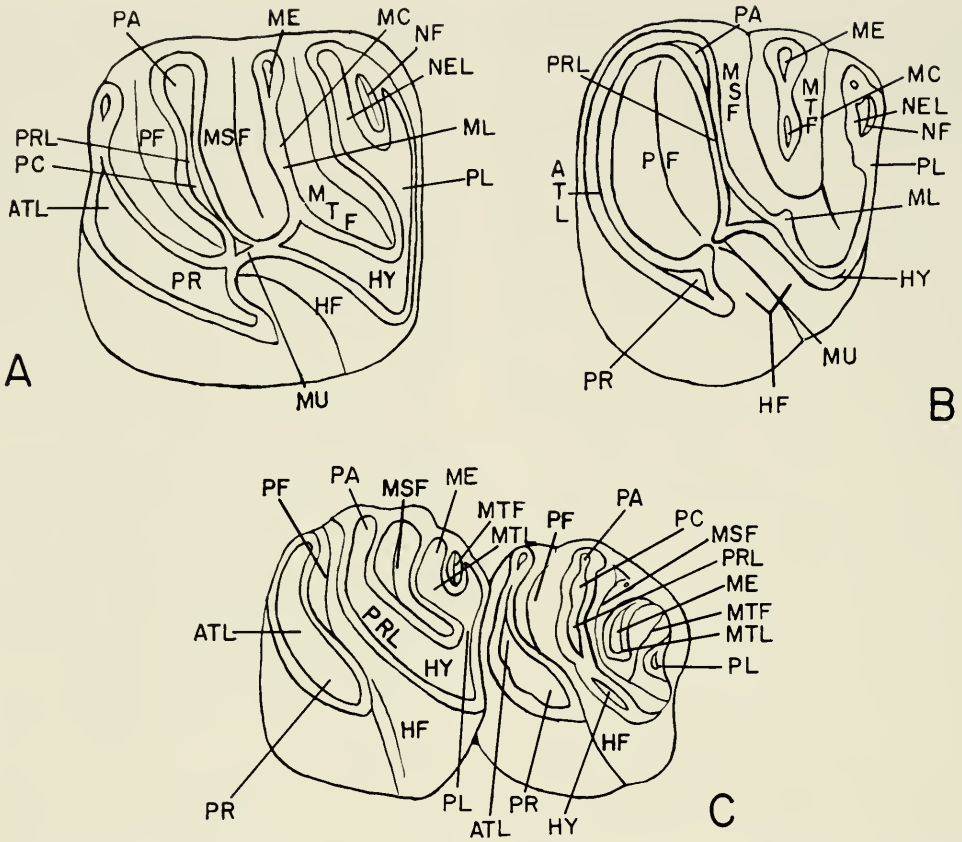

Figure 1. Nomenclature of parts of caviomorph upper cheek teeth. Anterior ends of all teeth to the left. A. *Protosteiromys medianus*, $LM^{1 \text{ or } 2}$. B. *Protosteiromys medianus*, LM^{3}. C. *Incamys bolivianus*, LM^{2-3}.

Abbreviations: ATL—anteroloph; HF—hypoflexus; HY—hypocone; MC—metaconule; ME—metacone; ML—metaloph; MSF—mesoflexus or mesofossette; MTF—metaflexus or metafossette; MU—mure; NEL—neoloph; NF—neofossette; PA—paracone; PC—protoconule; PF—paraflexus or parafossette; PL—posteroloph; PR—protocone; PRL—protoloph. Flexi are unworn valleys that become fossettes with wear.

1). They date the beginning of the Oligocene at 37.5 m.y.b.p.

Most unfortunately, no radiometric dates are available for the Mustersan. The duration of the hiatus, undoubtedly long, between this Age and the Deseadan can only be guessed at; a reasonable estimate is that it lasted throughout most or all of late Eocene time and perhaps into earliest Oligocene as well. Absence of rodents—and of primates—in Mustersan and earlier deposits is the basis for the view that the earliest members of these orders to reach South America arrived at some time during the Mustersan-Deseadan hiatus. Just when they did so and whether or not they arrived at essentially the same time are questions that will remain unanswered until the hiatus is filled. (One small local fauna of very peculiar facies, the Divisadero Largo, which contains no rodents or primates, is pre-Deseado and post-Musters.) The new Bolivian evidence of course does not directly contribute to determining the time, within the hiatus, when the rodents reached South America.

Hoffstetter and Lavocat (1970) did not

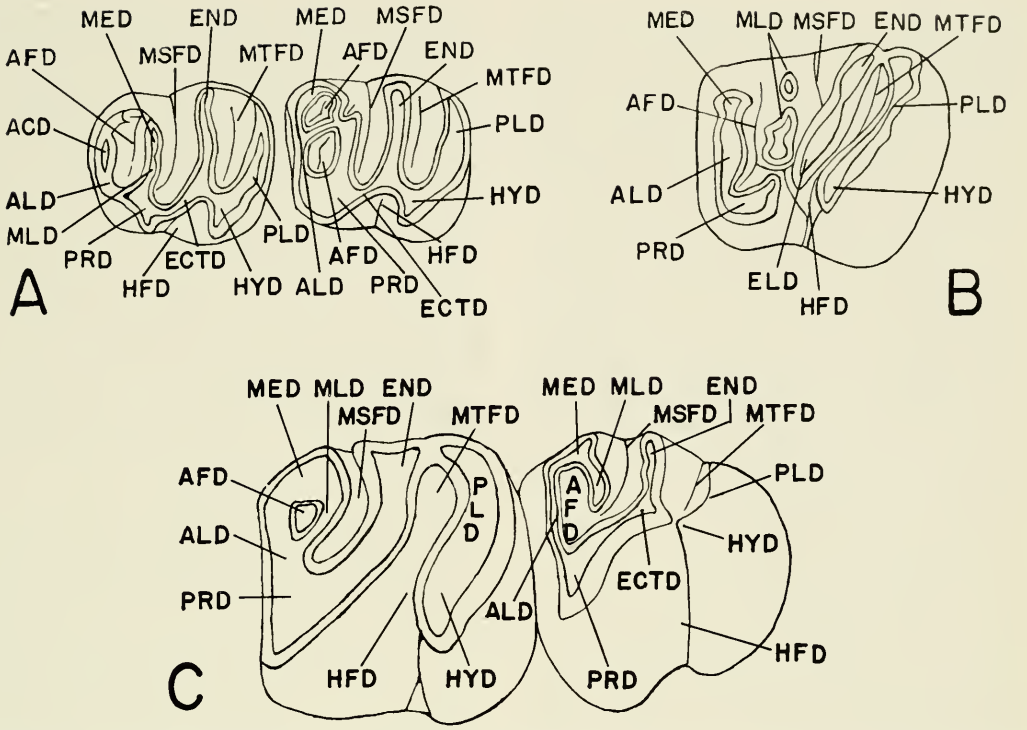

Figure 2. Nomenclature of parts of caviomorph lower cheek teeth. Anterior ends of all teeth to the left. A. *Migraveramus beatus*, RP_4–M_1, reversed. B. *Incamys bolivianus*, LP_4. C. *Incamys bolivianus*, LM_{2-3}.

Abbreviations: ACD—anteroconid; AFD—anterofossettid; ALD—anterolophid; ECTD—ectolophid; END—entoconid; HFD—hypoflexid; HYD—hypoconid; MED—metaconid; MLD—metalophid or metalophulid II; MSFD—mesoflexid; MTFD—metaflexid or metafossettid; PLD—posterolophid; PRD—protoconid. Flexids are unworn valleys that become fossettids with wear.

allocate their three new genera from Salla to families. Hartenberger (1975) placed *Sallamys* in the Octodontoidea, *Incamys* in the Chinchilloidea, and *Branisamys*, with a query, in the Dinomyidae. We had independently arrived at broadly similar conclusions (cf. Patterson and Pascual, 1972: 278), and present evidence in the following pages that *Sallamys* was a member of the Echimyidae, *Incamys* of the Dasyproctidae, and *Branisamys* of the Dinomyidae—without query. A new genus, *Migraveramus*, is referred to the Octodontidae. One specimen of Lavocat's hypodigm of *Incamys bolivianus* represents, we believe, an undescribed dasyproctid genus. Salla thus adds a family to the six previously represented in the Deseadan. In 1959 we inadvertently cited seven families on page 389, thus contradicting our correct statement on page 284 (with Lavocat, we are unable to agree that Hartenberger's *Villarroelomys* is referable to the Hydrochoeridae). Lavocat (1976) also placed *Sallamys* in the Echimyidae and *Incamys* in the Dasyproctidae, but erred, we believe, in also including *Branisamys* in that family. Hoffstetter and Lavocat (1970), on the basis of some points of similarity in cheek tooth structure between these forms and the approximately contemporaneous Fayum rodents, favor descent of caviomorphs from (as yet unknown) African Eocene thryonomyoids, which they believe to have been rafted across a then

narrower South Atlantic Ocean. This suggestion has been further elaborated upon by Lavocat (1973, 1976). We do not find the evidence presented in support to be any more convincing than we did a few years ago (Wood and Patterson, 1970). This and related topics are treated at some length in the concluding sections.

Cheek tooth terminology is as previously employed by us (1959: 286–288, Fig. 1). The terminology is repeated, and somewhat enlarged, in Figs. 1–2; it differs in important respects from that adopted by Lavocat (1976), stemming from his belief that the more complex Deseadan caviomorph teeth are primitive and that the less complex ones are specialized, whereas we take the opposite point of view.

Measurements of hypsodont rodent teeth (both cheek teeth and incisors) may vary with the age of the animal and with the precise manner in which the measurements have been made. They were made, for this study, as previously described (Wood and Patterson, 1959: 288–289). We have been encouraged, however, by the fact that, while the coefficient of variation for our measurements is often high (Tables 3–4; Wood and Patterson, 1959: Tables 3–5), it is usually less than 10. The measurements that give the highest variation are transverse diameters of upper cheek teeth (Table 3), where the curvilinear eruption of the teeth often produces an elongate buccal shelf; the anteroposterior diameter of M_3, due to variation in the measurement of the long posterior slope because of loss of the alveolar rim behind the tooth; and the actual measurements (as opposed to the ratio) of the incisors, due to diametric enlargement of these teeth with age. The reasons behind the variability of the tooth measurements are discussed in more detail below (p. 416).

We have reviewed the classification of the Suborder Hystricognathi in the final part of our discussion. In this paper, we have made the explicit assumption that hystricognathy arose once in the evolution of the rodents, and that, therefore, all hystricognathous rodents are related, and are more closely related to each other than any are to other groups of rodents. There is some documentary support for this assumption, but it cannot be taken to have been demonstrated. However, if hystricognathy arose independently, several times, as parallelisms, it means that there is no justifiable basis, at the present time, for grouping rodents at the subordinal level, and that no attempts at determining relationships between larger taxonomic groups of rodents should be made until there is full documentation for the evolutionary sequences involved (see below, pp. 476–477).

For example, at the present time, there is no final proof that the various families of caviomorphs have a common South American ancestor. We believe that they did have such a common ancestry, but, since seven families were already present in the Deseadan, when the caviomorphs first appear, the conclusion that they were the descendants of a single invading stock is an unproven assumption on our part.

As we classify them (see below, pp. 522–523), the Old World hystricognaths are divided into three groups that, in our opinion, cannot at present be demonstrated to have had a common ancestry later than the Eocene franimorphs. The Hystricomorpha contain a single family and the Bathyergomorpha contain two families, one Asian and one African. The African Thryonomyoidea perhaps should be referred to the Hystricomorpha and perhaps deserve recognition as a separate infraorder, the Phiomorpha. Lavocat (1973, 1976) united all the Old World hystricognaths in the Infraorder Phiomorpha. To avoid the probability of confusion between our usage and that of Lavocat, we have avoided using the infraordinal terms Phiomorpha, Bathyergomorpha, and Hystricomorpha, and have, instead, used the suprafamilial or familial terms, everywhere except in our

final section, Classification of the Suborder Hystricognathi.

The manuscript of this paper had been largely completed at the time of the death of the senior author. All of the first half—Taxonomy and Morphology—was in order; the various sections of the Discussion had been written, although some were not in their final form and, in some instances, no final decision had been reached as to their sequence. Extensive notes by Patterson were also available. In general, it is Wood's belief that the statements in the discussion are the opinions of both authors, unless the contrary is explicitly stated. Some sections that had to be prepared essentially or entirely by Wood are so indicated. Any errors that may have developed in the final preparation of the paper must be assumed to be the sole responsibility of the junior author.

ACKNOWLEDGMENTS

We are deeply indebted to the late Professor Glenn L. Jepsen for permission to study the Salla collection in Princeton University, and to Drs. Vincent J. Maglio and Donald Baird for continuing courtesies in this connection. We have received assistance in a number of matters from: Professor Robert W. Fields, Geology Department, University of Montana, Missoula; Dr. J.-L. Hartenberger, Laboratoire de Paléontologie, Université de Montpellier; Dr. P. E. Vanzolini and Dr. Lindolpho R. Guimarães, Museu de Zoologia da Universidada de São Paulo; and Dr. John H. Wahlert, then of the American Museum of Natural History. Dr. J. J. Raab, DDS, of Cape May Court House, N.J., made the X-ray photograph of the specimen of *Sallamys pascuali* described below (p. 383), and Dr. Luiz Fernando da Castro Leite, C. D., of São Paulo, made those of *Chaetomys* discussed on p. 394. Professor Elwyn L. Simons and Dr. Grant E. Meyer have generously contributed information about the Yale Fayum collections. Dr. Hartenberger has provided us, through the courtesy of Dr. Lavocat, with the numbers of specimens of various taxa of rodents included by the latter in his study of the Salla-Luribay rodents, data not given in the published report (Lavocat, 1976). Hartenberger stated (*in lit.*, 10 July 1976) that his own large collections of Salla rodents were still unidentified. We are grateful to Dr. R. W. Wilson of the Museum of Natural History, The University of Kansas, who has critically reviewed the manuscript and who has made a number of suggestions on points that needed clarification. We have attempted to carry out all of his suggestions.

The senior author had the benefit of numerous discussions with Dr. Ernest E. Williams of the Museum of Comparative Zoology, covering many aspects of the present paper. The major concrete suggestion here incorporated is that mentioned on p. 461, but there were many others of lesser fundamental import.

This study has been aided by awards to Wood of Grants 148 and 150 from the Marsh Fund of the National Academy of Sciences, and to Patterson from the Fundação de Amparo è Pesquisa do Estado de São Paulo. The drawings of Miocene thryonomyoids from Southwest Africa (Fig. 28G–K) were made by Wood during his tenure of a National Science Foundation Senior Post-Doctoral Fellowship in 1967–68. Illustration and publication have been aided by the Gordon Barbour fund of Princeton University. Continuing support has been received by Wood from the Biology Department, Amherst College.

ABBREVIATIONS

Abbreviations used for the names of museums:

ACM—Pratt Museum of Amherst College

AMNH—American Museum of Natural History

AMNH Mam—American Museum of Natural History, Dept. of Mammalogy
FMNH—Field Museum of Natural History
GB—Colección Geobol, La Paz
MACN—Museo Argentino de Ciencias Naturales
MCZ—Museum of Comparative Zoology
Munich—Institut für Paläontologie und historische Geologie, Universität München
MZUSP—Museu de Zoologia da Universidade de São Paulo
PU—Princeton University, Department of Geology
UCMP—University of California (Berkeley), Museum of Paleontology
YPM—Yale Peabody Museum

TAXONOMY AND MORPHOLOGY

Order **RODENTIA** Bowdich 1821
Suborder **HYSTRICOGNATHI** Tullberg 1899
Infraorder CAVIOMORPHA Wood and Patterson 1955 (in Wood, 1955, as a suborder)
Superfamily OCTODONTOIDEA Simpson 1945
Family OCTODONTIDAE Waterhouse 1839

Migraveramus[1] new genus

Diagnosis. Lower cheek teeth low crowned lingually and of medium height buccally, fully crested; dm_4 replaced at normal stage of life; P_4–M_2 fully tetralophate, with crests nearly perpendicular to anteroposterior axis; an anteroposterior crest crossing lingual part of anterofossettid; lower incisor with flat anterior face; coronoid process passing alveolar border at middle of M_3; angular process leaving body of ramus beneath middle of M_2; mental foramen in front of P_4, opening anteriorly and ventrally.

[1] The pluperfect of *migrare*, to migrate, plus *mus*, a rodent, in indication of our belief that this genus is closely related to the caviomorphs that first migrated to South America.

Type Species. Migraveramus beatus.

Distribution. Deseadan Oligocene of Bolivia.

Migraveramus beatus[2] new species
Figure 3

Diagnosis. As for the genus; measurements as given in Table 1.

Type. PU no. 21948, partial right ramus with P_4–M_2 and the base of the incisor, Braniša field no. 6515.

Hypodigm. Type only.

Horizon and Locality. Deseadan early Oligocene, lower part of Estratos de Salla; Salla-Luribay Basin, Bolivia.

Description. The three anterior lower cheek teeth (P_4–M_2; Fig. 3A) are all four-crested. For terminology of parts of teeth, see Fig. 2. The anterofossettid is crossed, on all, by an anteroposterior crestlet of varying prominence, arising from the anterolophid and reaching the lingual tip of the metalophid (Fig. 3A). The metalophid does not unite directly with the metaconid, but with a crest running buccally from it. On M_2, the connection has just been established (Fig. 3A). The lingual part of the anterofossettid basin is very shallow, and would be eliminated with but little wear. The protoconid is set off from the ectolophid by an angulation on P_4. A distinct anteroconid is present on this tooth (Fig. 3A). There is no trace of a mesoconid or mesolophid on any of the teeth. The hypolophid is connected with the hypoconid by a narrow isthmus arising from the front of the latter. It is marked by a swelling midway between the ectolophid and entoconid. The posterolophid shows indications of there having been a hypoconulid. The anterofossettid is closed lingually; the mesoflexid and metaflexid are open on all three teeth, the mesoflexid being the deeper; the hypoflexid is the deepest of all. The buccal cusps are somewhat higher than the lingual ones; there is little difference in height between the an-

[2] Named for the Little Angel.

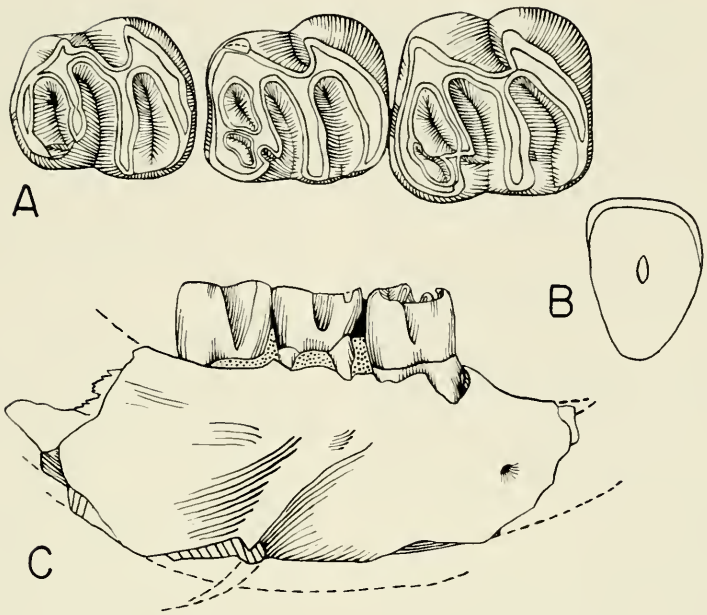

Figure 3. Teeth and jaw of *Migraveramus beatus*, gen. et sp. nov., PU no. 21948, type. A. RP_4–M_2, ×10. B. Cross section of RI_1, beneath diastema, ×10. C. Lateral view of right lower jaw, ×5.

terior and posterior cusps of each side. The base of the enamel is nearly horizontal around the teeth. The anterior root of dm_4 is still present in front of P_4 (Fig. 3C).

The incisor has a flat anterior face, with the enamel extending fairly far around on both sides (Fig. 3B). The pulp cavity, below the diastema, is small and oval.

The mandible is badly damaged. No features of any significance were observed on the medial side. The mental foramen (Fig. 3C) is about half way up the side of the mandible, a short distance in front of the anterior root of P_4, and faces forward and downward. The anterior tip of the masseteric crest lies on the upper third of the mandible, beneath the rear of P_4, whence it curves posteroventrad and increases rapidly in prominence. Only the beginning of the coronoid process is visible, but it passed the alveolar border near the front of M_3 (Fig. 3C).

Relationships. The mandible agrees with that of the Deseadan octodontid *Platypittamys* (Wood and Patterson, 1959: 298) in the absence of any distinct scar for the *M. masseter medialis, pars anterior*, suggesting that this muscle was poorly developed.

The pattern of the lower molars agrees with that of *Platypittamys* alone among Deseadan rodents—there are four transverse crests, the two anterior and the two posterior being widely separated by the deep mesoflexid (Wood, 1949: Fig. 3C,D). As in *Platypittamys* (Wood, 1949: Fig. 3C; M_2), the metaconid is somewhat isolated from the metalophid. The

TABLE 1. MEASUREMENTS, IN MM, OF TEETH OF *Migraveramus beatus*, TYPE, PU NO. 21948, RIGHT.

P_4 anteroposterior	2.38	M_2 anteroposterior	2.48
width, metalophid	1.74	width, metalophid	2.53
width, hypolophid	2.14	width, hypolophid	2.49
M_1 anteroposterior	2.40	I_1 anteroposterior	2.16
width, metalophid	2.02	transverse	1.50
width, hypolophid	2.26	ratio	.70

anteroposterior bar across the anterofossettid also appears in *Platypittamys* (Wood, 1949: Fig. 3D). The pattern of P_4 of the two genera, however, is quite distinct, that of *Migraveramus* being fully molariform, whereas P_4 of *Platypittamys* has no trace of a posterolophid, and the anterior half is not so molariform as in *Migraveramus*.

The cheek teeth of *Migraveramus* are appreciably higher crowned than those of *Platypittamys*.

The incisor (Table 1) is considerably wider than that of *Platypittamys* (width/length ratio = .70 as opposed to .39 and .57 in the two specimens of *Platypittamys* given by Wood, 1949: Table 2). The general shape of the incisors, is, however, identical.

Wood and Patterson (1959: 295) agreed with Wood (1949: 45) that *Platypittamys* and its relatives (the primitive octodontids, of which *Platypittamys* was then the only Deseadan representative) were "ancestral, at least structurally, to all rodents . . . included in the Caviomorpha, with the possible exception of the Erethizontidae." We still take this position, and feel certain, among other things, that the teeth of *Migraveramus* are completely different from those of any thryonomyoid and demonstrate the origin of the Caviomorpha from a tetralophate ancestry, of the type found during the middle and late Eocene in North American rodents, including franimorphs as well as paramyids and sciuravids. The same pattern is found in the latest Eocene and Oligocene ischyromyids.

The significance of the peculiar pattern of P_4^4 of *Platypittamys* is still uncertain. Incidentally, it should be mentioned that the "recently discovered but still undescribed lower Gray Bull paramyid" cited by Wood and Patterson (1959: 296) in this connection, is *Franimys amherstensis* from the latest Paleocene Clark Fork beds, the earliest known hystricognath rodent. The fully molariform premolar of *Migraveramus* suggests that the ancestral stock of the caviomorphs may have had tetralophate premolars as well as molars, agreeing in this with the Eocene and Oligocene North American forms mentioned above. This is supported by the fact that, in a completely unrelated group of rodents, a somewhat analogous pattern of P_4 occurs, clearly as the result of secondary reduction of complexity (*Meliakrouniomys*, Wood, 1974a: 79–80, Fig. 33C).

We conclude that the octodontids are the most primitive of the Deseadan rodents, and that the nearest known approach to the ancestral condition is represented by *Migraveramus*.

Family ECHIMYIDAE Gray 1825

We believe that this family should be dated from Echimyna Gray 1825, the first usage covering the modern family in essential concept though not in spelling, rather than from Waterhouse 1839.

Subfamily HETEROPSOMYINAE Anthony 1917

Sallamys Hoffstetter and Lavocat 1970

Emended Diagnosis. Infraorbital foramen and area of origin of *M. masseter medialis, pars anterior* large (Hoffstetter and Lavocat); cheek teeth brachydont, uppers higher lingually than labially, lowers higher labially, both about as in Paramyidae and Reithroparamyidae; dm_4^4 replaced; dm^3 possibly present; P^4 variable, trilophate or incipiently tetralophate, with or without mure, paracone and buccal tip of anterocone distinct in early stages of wear; M^{1-3} notably wider than long, tetralophate with lophs directed transversely, metafossette shallow; P_4 with fully formed hypolophid, small metalophid spur, metaconid distinct in early stages of wear; M_{1-3} basically trilophate with minute vestiges of metalophid; anterolophid, hypolophid and lingual portion of posterolophid transverse; dm_4 replaced in normal manner, very

complex, with two labial, one anterolabial, two lingual flexids.

Type Species. *Sallamys pascuali* Hoffstetter and Lavocat 1970.

Distribution. Deseadan Oligocene of Bolivia.

Sallamys pascuali Hoffstetter and Lavocat 1970
Figures 4–5

Diagnosis. As for the genus. Tooth measurements as given in Table 2.

Type. Anterior part of skull, preserved back to the glenoid on the left side, with articulated jaw and including a complete set of cheek teeth, in "ma collection personelle, déposée à l'Institut de Paléontologie du Muséum Nationale d'Histoire Naturelle, à Paris" (Hoffstetter, 1976: 13); listed without museum number by Hoffstetter and Lavocat (1970: 174) and without museum reference as "SAL 101A (Crâne) et SAL 101B (Mandibule)" by Lavocat (1976: 23).

Referred Material. Eleven specimens in the Princeton collections, listed in Appendix 1 (p. 528).

Horizon and Localities. Deseadan, early Oligocene, lower part of Estratos de Salla, Salla-Luribay Basin, Bolivia. PU nos. 20906–20911 were found at Pampa Tapial in a grayish-white, gypsiferous clay some 10 m above a 30–50 cm thick bed of greenish-gray limestone, within an area 20 by 20 m; PU nos. 20912–20913 are from dark red to reddish-brown rocks in the lower part of the Salla succession; and PU nos. 20982 and 21727 are from Tomolo (so spelled by Braniša) midway between Salla and Aroma (L. Braniša, field notes). We doubt whether Tomolo is the same as the locality identified by Hoffstetter as Toloma (1976: Fig. 2), since Hoffstetter stated (1976: 14) that he found no rodents at Toloma.

Description. Beyond stating that the infraorbital foramen was large and that the area of origin of *M. masseter medialis, pars anterior* was extensive, Hoffstetter and Lavocat (1970: 173) gave no account of cranial structure. The skull was, however, described in detail by Lavocat (1976: 24–26).

The material at our disposal of course reveals very little of the skull structure. The maxillary fragment shows no trace of an alveolus for P^3. There is, however, a slight elevation on the curved surface of the maxilla anterad and slightly mesiad of the anterobuccal root of P^4 (Fig. 4A; X). When viewed with the light shining from the correct angle, this area is seen to have quite a different luster from that of the adjacent areas of bone, and to be bifid posteriorly. This area may represent the closed alveolus of a shed dm^3, a tooth now known to occur in some Deseadan caviomorphs. An X-ray photograph shows that this area is clearly differentiated from the adjacent bone, but that there is no identifiable tooth structure.

The zygoma arises from the maxilla anterior to P^4 as in echimyids generally, and the ventral surface of the maxilla ascends abruptly anterior to P^4. Medial to this tooth is a concavity (Fig. 4A; IF), which is the posterior end of a very elongate incisive foramen that reaches back to the middle of P^4, farther than Lavocat (1976: 26) was able to trace the foramen, since this area is still buried in matrix in the type (Lavocat, 1976: Pl. 1, Fig. 3). The foramen extends farther posterad than in any of the Santa Cruz rodents figured by Scott (1905), or than in any of the other known Deseadan caviomorphs except *Incamys* (Fig. 14A). There are similarities to that of *Metaphiomys*, although it is not sunk in a palatal depression, as is the case in the Fayum form (Wood, 1968: Fig. 6A). The dorsal view of the maxillary fragment shows the passage of the sphenopalatine foramen (Fig. 4B; SPF), running anteromesially from the orbit to the nasal passage. The lateral wall of the nasal passage, anterior to the sphenopalatine foramen, contains a groove that runs as far forward as the bone is preserved (Fig. 4B; NLC?). This is believed to be

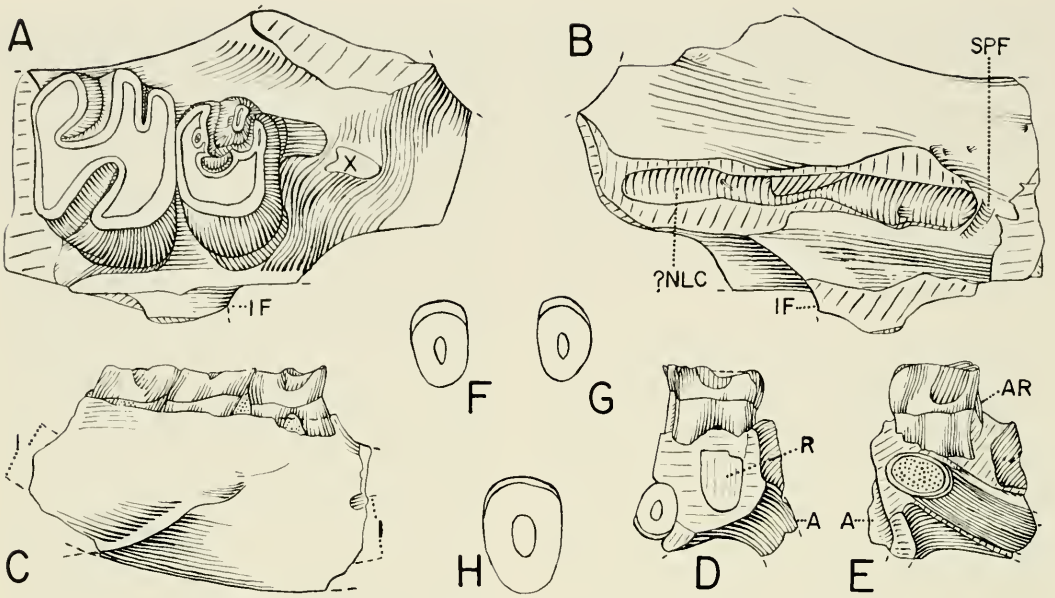

Figure 4. Teeth and bones of *Sallamys pascuali*. C–E. ×5; others, ×10. Dotted areas are matrix. A–B. Maxillary fragment containing RP^4–M^1, PU no. 20906. A. Occlusal view, anterior end to the right. B. Dorsal view, anterior end to the left. C. Lateral view of lower jaw, PU no. 20907, with anterior part of diastema, mental foramen, angular process and incisor added from PU no. 20911. D–E. Anterior and posterior ends of PU no. 20912. D—anterior view, broken through posterior root of P_4; E—posterior view, broken just behind M_2; F–H. Cross sections of lower incisors, seen from the front. F. PU no. 20913, LI_1, below diastema. G. PU no. 20909, RI_1, below front of dm_4. H. PU no. 20912, LI_1, below front of M_1.

Abbreviations: A—angular process; AR—anterolingual root of M_2; I—projection of position of incisor; IF—posterior end of incisive foramen; NLC?—?nasolacrimal canal; R—posterior root of P_4; SPF—sphenopalatine foramen; X—possible unerupted dm^3 within the bone.

the nasolacrimal canal, which apparently descended vertically from the lacrimal foramen, above M^1, and then turned abruptly forward. This groove is separated from the sphenopalatine foramen by a wall of bone in PU no. 20906 (Fig. 4A). If this is the nasolacrimal canal, its course was quite different from that in *Incamys*, in which it seems to have followed a straight line from the lacrimal foramen to the nasal passage. In *Branisamys*, the canal curved more ventrally than in the other genera, and extended forward as a distinct passage (Figs. 24A, 25B). Three small nutritive foramina are present in the floor of the orbit, just anterior to the sphenopalatine foramen. There is a shallow groove on the floor of the infraorbital foramen, presumably marking the course of the infraorbital nerve and blood vessels.

The masseteric crest of the mandible arises high on the horizontal ramus beneath the posterior part of P_4 (Fig. 4C), and becomes very large as it runs downward and backward. Anteriorly, the incisor lies mesiad of the roots of the cheek teeth (Fig. 4D); but, farther back, the incisor curves laterad and crowds the posterior root of M_2 (Fig. 4E) and all the roots of M_3. This is accompanied by a spiral twisting of the incisor (Fig. 4D–E). The exact location of the mental foramen caused us some uncertainty. In PU no. 20907, the break at the anterior end of the bone passes through what looks like a

small mental foramen very high on the bone. However, in PU nos. 20908, 20911 and 20913, there clearly is a fair-sized foramen, just in front of P_4, slightly above the middle of the lateral side of the mandible, and at the level of the upper edge of the incisor. There are several nutrient foramina on the medial surface of the jaw below the molars and above the incisor. In the contemporary *Xylechimys* and *Deseadomys arambourgi* (but not in *D. loomisi*) the masseteric crest begins beneath M_1, and in *D. arambourgi* there are two mental foramina, the posterior beneath the middle of P_4 (no such foramen is present in any of our specimens of *Sallamys pascuali*) and the anterior beneath the middle of the diastema, somewhat farther forward than in *D. arambourgi* (Wood and Patterson, 1959: Fig. 6).

The cheek teeth, notably the uppers, increase in width posteriorly, to M_2^2. For terminology of the parts of the cheek teeth, see Figs. 1–2 (pp. 376–377). According to the illustrations given by Hoffstetter and Lavocat (1970) and by Lavocat (1976: Pl. 1, Fig. 5), M_3^3 are slightly smaller than M_1^1 (Lavocat, 1976, unfortunately gave no measurements except the length of the tooth row for any of the Salla rodents, stating, on page 22, that he had not included other measurements because Hartenberger was working on a statistical study). The teeth are brachydont, although the uppers show some unilateral hypsodonty, the height of crown on the lingual side being about twice that on the labial (Fig. 5B). The base of the enamel is essentially horizontal around the tooth. As indicated below, in our opinion the teeth are clearly four-crested (Fig. 5A). Lavocat (1976: 29–30) describes these teeth as four-crested, but believed that he could find the remnants of a fifth, the mesoloph (see below, p. 386). On a subsequent page, however, he concluded that *Sallamys* showed "clairement un morphologie pentalophodonte" (1976: 43), which seems to us to be stretching a point.

In the lower teeth, the crown is highest at the hypoconid, but the disparity in height of various parts of the crown is less pronounced than in the uppers. The molars are wider relative to length than in *Deseadomys*, resembling those of *Platypittamys* in this respect and also in the very transversely directed lophs and lophids. Except as noted below, our descriptions of the teeth are based on the Princeton specimens.

The contour of P^4 is oval, and the tooth is notably smaller than M^1 (Fig. 4A). Anteroloph, protocone and posteroloph sweep around the anterior, lingual and posterior faces of the tooth, and a slight vertical depression on the lingual face (too faint to show on Fig. 4A except as an irregularity of the enamel-dentine border) may perhaps mark an exceedingly incipient separation of a hypoflexal division. Lavocat (1976: 29) did not see such a depression, and none shows on his stereophoto (*op. cit.*: Pl. 1, Fig. 5). The labial extremity of the anteroloph closely approaches the paracone, from which it is separated by a shallow notch; with a little more wear the two would have united. The paracone is large, elongate transversely and independent, the protoloph being incomplete. As a result of this, the paraflexus and the mesoflexus are confluent, forming a deep U-shaped fossa in the center of the tooth. This is partially divided by a thin, low ridge—the serial homolog of the mure of the molars—connecting a spur from the protocone to one from the posterior crest and isolating a deep central basin. This ridge is absent on the type (Lavocat, 1976: Pl. 1, Fig. 5). The posterior crest is rather wide in its labial half, where it contains a small fossette, the serial homolog of the molar metafossette. The tooth is thus incipiently tetralophate and, for an echimyid, is advanced for its time in this feature. Hoffstetter and Lavocat state that, in

the type, there is a "vestige" (rudiment, in our opinion) of the metaloph on the anterior face of the posteroloph, but this is not shown in their figure. Their figure does, however, show a small crest on the posterior side of the protoloph (1970: Fig.), which we believe to be homologous to what we interpret as the mure (Fig. 4A). However, Lavocat (1976: 20) does not mention either structure, and his stereophoto (*op. cit.*: Pl. 1, Fig. 5) shows neither one.

In this respect, P^4 of PU no. 20906 is at once more and less advanced than in contemporary octodontoids. It is more advanced than that of the type (Hoffstetter and Lavocat, 1970: 173, Fig.) in the complete incorporation of the anterocone in the anteroloph, the presence of the mure, the fossette in the posteroloph, and the incipient lingual division. It is less advanced than those of *Platypittamys* and *Deseadomys arambourgi* in the isolation of the paracone; more advanced than either in the incipient division of the posteroloph; and more advanced than *Platypittamys* in the possession of a mure. What all this indicates, we suspect, is merely that octodontoids, and indeed all caviomorphs, were actively undergoing molarization of the premolars during Deseadan time and that the process was accompanied by much individual and populational variation. This definitely indicates, to us, that the ancestral caviomorph stock did not have fully molarized upper premolars.

The first upper molar of PU no. 20906 (Fig. 4A) is worn in a manner slightly different from that of the corresponding tooth of the type. The metafossette has been worn away, and the paraflexus has been reduced to a very shallow groove, although it is deeper than in the type (Lavocat, 1976: Pl. 1, Fig. 5). The hypoflexus is still much more widely open than is shown by Hoffstetter and Lavocat (1970: Fig.) or by Lavocat (1976: Pl. 1, Fig. 5). The deep mesoflexus turns posteriorly at its lingual extremity, revealing that, as in M^1 of the type, the metaloph had shifted its moorings from the mure to the posteroloph. In the type, but not in the Princeton specimen, the former site of metaloph attachment is marked by a minute projection on the mure. Lavocat (1976: 30) discussed this projection as "un portion linguale rudimentaire du mésolophe," an interpretation that seems to us to be without justification. The crestlet is aligned with and points toward the metacone, which should not be true of a mesoloph. It lies well behind the middle of the mure, whereas a mesoloph normally lies at the center of the mure. Lavocat pointed out that there is a low ridge, below the wear surface of M^1 of the type, that connects the metacone and what he considers the rudiment of a mesoloph. This low ridge is not present in the Princeton specimen. The presence of this ridge would seem to us to demonstrate that the entire assemblage is a metaloph, which would disprove Lavocat's assertion that this ridge strengthens the evidence for the existence of a mesoloph.

The isolated left upper molar, PU no. 20982 (Fig. 5A), is probably LM^1 rather than LM^2 because (by comparison with Hoffstetter and Lavocat, 1970: 173, Fig.) the relationships of the three measurements are closer to those of M^1 than to those of M^2. Moreover, Lavocat's illustration of the type (1976: Pl. 1, Fig. 5) shows a complete metaloph on M^2 and an interrupted one on M^1. The Princeton tooth is clearly a molar because of the wear facet on the anterior face (Fig. 5B). The width of the posterior half (Table 2) shows that it cannot be M^3. The absence of a wear facet on the posterior face is because this tooth was newly erupted at the time of its owner's death, and the next succeeding tooth had not yet come into contact with it. This tooth is less worn than any tooth figured by Hoffstetter and Lavocat (1970) or by Lavocat (1976), and clearly shows (Fig. 5A) the unworn pattern, essentially as described in the previous paragraph.

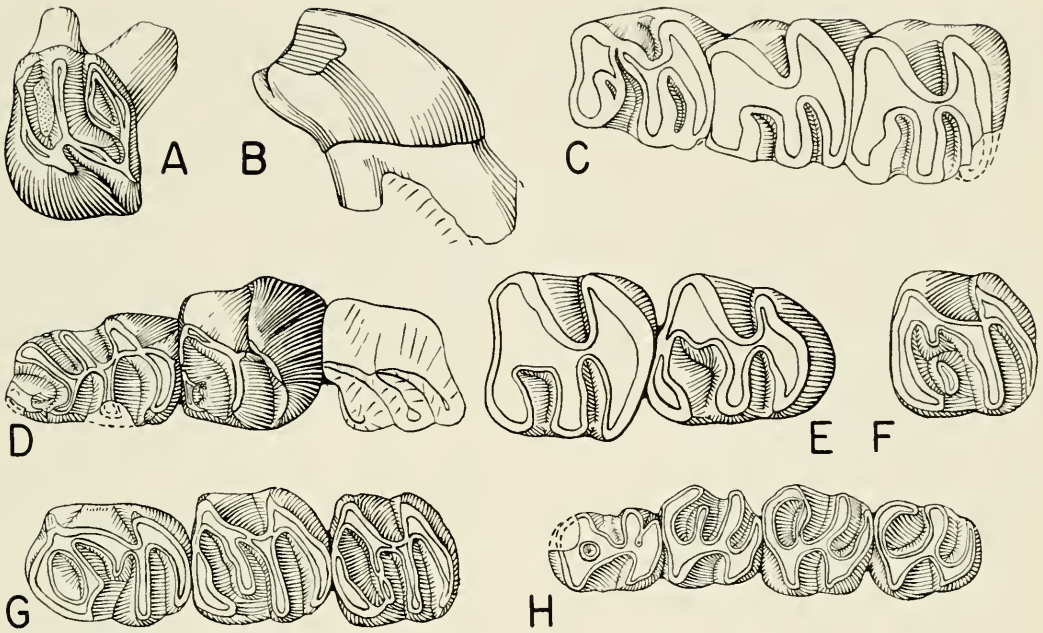

Figure 5. Cheek teeth of *Sallamys pascuali*, *Protacaremys prior*, and *Prospaniomys priscus*. H., ×5; others, ×10. A–B. *Sallamys pascuali*, PU no. 20982, LM^1. A. Occlusal view. Dotted area is matrix. B. Anterior view, showing unilateral hypsodonty. C. *S. pascuali*, PU no. 20907, RP_4–M_2. D. *S. pascuali*, PU no. 20909, Rdm_4–M_2. Unerupted M_2 with no enamel cap or, at most, an incomplete one. Grooves are in dentine. E. *S. pascuali*, PU no. 21727, RM_{2-3}. F. *Protacaremys prior*, FMNH no. P 13295, RM_1. G. *Protacaremys prior*, AMNH no. 29707, Rdm_4–M_2. H. *Prospaniomys priscus*, AMNH no. 29697, Ldm_4–M_3.

There are only four crests, with not the slightest suggestion of a fifth. The third (the metaloph) is firmly attached to the posteroloph and isolated from the hypocone, although there is a crestlet from the hypocone, running posteriorly across the mesoflexus, at right angles to the direction of what Lavocat (1976: 30) described as a rudimentary mesoloph. The tooth is supported by three roots, two buccal and one lingual. The lingual side of the tooth has about twice the height of the buccal.

The last two upper molars are not represented in the Princeton collection. The published figures and description show that the third loph, the metaloph, has the usual attachment to the mure, and, surprisingly, that the hypoflexus of M^2 was converted by wear to a hypofossette earlier than on M^1. Evidently there was individual variation in depth of flexus as well as in angle of wear.

The last upper molar, as figured by Lavocat (1976: Pl. 1, Fig. 5) seems to us to have a structure completely homologous to that of the anterior molars, with a complete metaloph followed by a complete posteroloph. The latter bends toward, but does not reach, the metaloph. This identity of structure among the molars seems to us clearly to demonstrate the accuracy of our interpretation. We continue to feel that there is no possible basis for assuming, as does Lavocat, that the four-crested upper teeth of *Sallamys* can be interpreted as "structures pentalophodontes" (Lavocat, 1976: 30).

Lavocat's discussion of Wood's interpretation of the crests in *Sallamys* (Lavocat, 1976: 30) seems rather confused,

since he comments on the crest considered by Wood to be the mesoloph. But Wood (1974b: discussion, Fig. 1) clearly indicated that, in his opinion, there is no mesoloph in any caviomorph, a position that we still maintain.

Lavocat (1976: 31) stated that the large size of the protocone and small size of the hypocone of the upper molars of *Sallamys* is a primitive condition, "plus proche du plan trigonodonte" than are the teeth of *Platypittamys*. We disagree with this conclusion; none of the Caviomorpha are very close to the trigonodont condition. The rodents that invaded South America must, we feel, already have had a well-developed hypocone. The difference in size of the protocone in *Sallamys* and *Platypittamys* arises from the greater lingual hypsodonty (an advanced character) of the former, which would permit a rapid enlargement of the protocone with wear. How this would occur is clearly shown in Fig. 5A.

According to Lavocat (1976: 31), "le sinus interne des molaires se ferme lingualement, avec l'usure, alors que les vallées externes sont encore bien ouvertes labialement." However, his stereophotograph of the type (1976: Pl. 1, Fig. 5) shows that there is no sequence of closure of the valleys that is consistent from tooth to tooth, and it seems evident that there is great individual variation both in the openness of the hypoflexus, paraflexus and metaflexus (see, for example, Fig. 5A, metaflexus) and the angle at which the wear surface cuts the teeth. This latter is highly variable because of the lingual hypsodonty, which resulted in rotational eruption of the upper teeth, albeit less pronounced than in *Incamys* (see below, pp. 416–418).

As Hoffstetter and Lavocat stated, the talonid of P_4 is completely molariform; a hypolophid as large as those of the molars is present, its lingual extremity joining the posterolophid to isolate a metafossettid. We have previously been in some doubt as to the identification of the posterior lophid of P_4 of echimyids and octodontids, and have tentatively identified it as the serial homolog of the molar hypolophid (Wood, 1949; Wood and Patterson, 1959: 307). Whatever the situation may be in the previously described forms, it would seem that, in *Sallamys* at least, the posterior crest should be called the posterolophid.

The above-cited molarization of the talonid is an advanced character for a Deseadan octodontoid; neither *Platypittamys* (Wood, 1949: Fig. 3C–D) nor *Deseadomys arambourgi* (Wood and Patterson, 1959: Fig. 5A) shows any trace of it. Anteriorly, in the type of *Sallamys pascuali* (Lavocat, 1976: Pl. 1, Fig. 6), the rather stout metaconid has not quite fused with the protoconid, and a short metalophid spur (identified by Lavocat, 1976: 31, as more probably a mesolophid) projects posterolingually from the protoconid; the whole is rather similar to the trigonid area of *D. arambourgi*. In the somewhat more worn PU no. 20907 the protoconid and metaconid are united, but the metalophid spur is still clearly visible, running to the posterior margin of the protoconid (Fig. 5C). The position and relationships of the crest in this tooth seem to us to demonstrate that it cannot be a mesolophid. With a little more wear, this crest would lose its identity, and the tooth would become almost wholly molariform. The ectolophid bears an enlargement that looks somewhat like, but is not, a mesoconid (Fig. 5C). This feature is not present in P_4 of the type (Lavocat, 1976: Pl. 1, Fig. 6).

The lower molars are rather simple in structure, consisting of three essentially transverse lophids (the antero-, hypo-, and posterolophids) separated by deep meso- and metaflexids, and of anterolabially directed, moderately acuminate protoconid and hypoconid separated by a deep hypoflexid (Fig. 5C–E). This last is by far the deepest of the folds, but, due to the oblique manner of wear, all three folds were evidently obliterated at about

TABLE 2. MEASUREMENTS, IN MM, OF TEETH OF *Sallamys pascuali*.

Lower teeth

PU nos.	20907 R	20908 R	20909 R	20910 R	20911 L	20912 L	20913 L	21727 R	21950 R	N	$\bar{X}$
P_4–M_3 anteroposterior								8.70		1	
P_4 anteroposterior	1.92		d2.32							1/1	
width metalophid	1.41		d1.21							1/1	
width hypolophid	1.84		d1.47							1/1	
M_1 anteroposterior	1.84	1.92	1.89	1.98		2.00			2.10	6	1.96
width metalophid	1.87	2.01	1.69	1.88		2.03			1.97	6	1.91
width hypolophid	1.97	1.96	2.03	2.06		2.15			2.20	6	2.06
M_2 anteroposterior	1.81	ca. 2.0	ca. 1.9		1.93	2.14		2.17	2.38	7	2.05
width metalophid	2.22				ca. 2.3	2.32		2.18		4	2.24
width hypolophid	2.21				ca. 2.4	2.39		2.21	2.48	5	2.34
M_3 anteroposterior								2.39		1	
width metalophid								1.98		1	
width hypolophid								1.74		1	
I_1 anteroposterior		1.66	1.13			1.53	1.16	1.73	1.51	6	1.45
transverse		1.07	0.75			1.04	0.77	1.27	1.07	6	1.00
ratio		.62	.67			.68	.66	.73	.71	6	.68

Upper teeth

PU no.	20906 R	PU nos.	20906 R	20982 L
P^4 anteroposterior	1.45	M^1 anteroposterior	1.88	1.84*
width protoloph	2.12	width protoloph	2.65	2.33*
width metaloph	2.04	width metaloph	2.21	2.22*

d = deciduous tooth (dm_4).
* possibly M^2.

the same time, the occlusal surfaces ending up as featureless quadrangles surrounded by a continuous wall of enamel. Even in the highly worn teeth of PU nos. 20908 and 20911, the anterior enamel, although greatly thinned by interdental wear, is still continuous across the front of the tooth. An unworn M_1 (PU no. 20909, Fig. 5D) shows that there was no trace of anything that could possibly be imagined as a mesolophid; that all crests were thin and continuous upon eruption; and that there are minute irregularities, which can only be vestiges of the posterior arm of the metaconid, near the center of the upper half of the posterior face of the anterolophid. This seems to show on M_3 of the type (Hoffstetter and Lavocat, 1970: 173, Fig.; Lavocat, 1976: Pl. 1, Fig. 6), but to have been eliminated by wear on M_3 of PU no. 21727 (Fig. 5E). M_3 narrows posteriorly.

An unerupted M_2 is present in PU no. 20909. It lacks the entire enamel cap, and shows the tooth pattern only in dentine. The pattern seems to have been identical to that of M_1 of the same specimen (Fig. 5D), and again there clearly was no mesolophid. There is a series of radiating furrows in the dentine, which may have marked the attachment of the enamel cap, or which may be shrinkage cracks in the dentine. More worn specimens of M_2 (Fig. 5C,E) likewise show a pattern indistinguishable from that of M_1.

The incisor in PU no. 20913 (Fig. 4F) is crowded against the posterior root of M_2, and the curvature is such that the crowding would have been even greater beneath M_3. This is confirmed by the edentulous fragment of a left ramus, PU no. 20913, in which the roots of M_3 are small, crowded and exceedingly short, because of interference by the incisor.

These observations suggest that M_3 may have been very variable in this species, and in process of reduction.

A little worn, essentially complete dm_4 is present in PU no. 20909 (Fig. 5D); it is a complex tooth. Appreciably longer than any of the molars, it tapers forward rather rapidly. The trigonid and talonid slope down toward the ectolophid, which is worn. A possible explanation of this state of affairs, unusual in so lophate a rodent tooth, is that dm^3 was present, as in *Incamys* and *Branisamys*, and that this tooth and dm^4 formed a wedge when newly erupted, with dm^3 opposing the anterior third of dm_4, and dm^4 opposing the posterior two thirds. There are two buccal, one anterobuccal and two lingual flexids. The identities of the various lophids separated by these flexids (and hence those of the flexids) can be determined by comparison of dm_4 in various Deseadan and Colhuehuapian caviomorphs, as discussed below (pp. 500–501). The talonid is molariform. The large hypoconid was separated by notches from the posterolophid and hypolophid when the tooth was freshly erupted, to judge from its very constricted connections in the specimen. The metaflexid is large and deep, and would convert to a fossettid with extreme wear. Anterior to the point of divergence of the transverse hypolophid, the sinuous, centrally situated ectolophid gives off a labially directed lophid that parallels the angulate labial extension of the hypoconid. The deep flexid between them is the hypoflexid, and the anterior lophid is probably the serial homolog of the molar crest between protoconid and ectolophid that has here parted company with the protoconid. The flexid between this neomorph labial lophid and the protoconid is also a neomorph; it is a little shallower than the hypoflexid, and a minute cuspule is situated at its buccal extremity, probably a remnant of the ancestral marginal crest in this area. Immediately anterior to the point of junction with this neomorph labial lophid, the ectolophid runs anterointernally to fuse with one crest running posterointernally from the protoconid and with another shorter one running posteroexternally from the metaconid. The latter is the serial homolog of the metalophid, while the former is what we have elsewhere (Wood and Patterson, 1959: 288) called the neolophid. The anteroconid is a large cusp that still retains much of its individuality. A slight notch separates it from the metaconid, a much deeper one from the protoconid, and there is a posterior extension, directed toward the ectolophid, which may be the initial stage in a connection of the anteroconid with this crest. The anterolabial flexid, lateral to the anteroconid, deepens toward the center of the tooth, and would presumably convert to a fossettid at a late stage of wear.

The lower incisor extends back to a point slightly behind and pressed against the roots of M_3. Anteriorly, it lies mesiad of the roots of the cheek teeth (Fig. 4D), and is oriented in the usual rodent manner, with the enamel cap (=anterior face) down. However, farther back the tooth rotates (Fig. 4E) so that, beneath the rear of M_2 or the front of M_3, the incisor is twisted, with the enamel cap directed mesiad. Where this takes place, the tooth presses against the posterior root of M_2 (Fig. 4E) and all three roots of M_3 (PU no. 20913), greatly reducing their lengths. The incisor is rather small (Table 2), slender and oval in outline, the posterior portion being very little narrower than the anterior face. The anterior face is smooth and gently convex (Fig. 4E–H). The enamel extends over approximately half of the lateral face and over about a third of the medial. Unfortunately, it was impossible to obtain measurements of the rear end of the incisor of the juvenile PU no. 20909, due to breakage, so that we have been unable to determine the rate of diametric growth of the tooth.

Relationships. As we have previously stated (1959: 300), the Deseadan mem-

bers of the Octodontidae and Echimyidae are very similar to each other in molar structure, and are separated formally only because their descendants diverged. From the Colhuehuapian on, the two families are distinguished by the retention of dm_4^4 in the Echimyidae and their replacement, ontogenetically, by P_4^4 in the Octodontidae. So far as known, there was no retention of dm_4^4 in Deseadan echimyids. Of the molar characters that we previously gave as separating the earlier members of the two families, *Sallamys* agrees with octodontids in two: the decidedly transverse alignment of the lophs and lophids and the width/length relationships. It agrees with echimyids in the somewhat deeper flexi and flexids and most importantly, in the loss of the metalophids. In this feature *Sallamys* is almost as advanced as *Deseadomys loomisi*, more advanced than *D. arambourgi*, *Xylechimys*, or the Colhuehuapian *Protacaremys* (Fig. 5F–G), *Prospaniomys* (Fig. 5H), and *Protadelphomys*. Loss or interruption of the metalophid is very rare in the molars of the earlier octodontids. Out of a rather large series of the Santacruzian *Sciamys principalis* in the Ameghino collection, only two show metalophid irregularities (MACN nos. A 1886 and A 4113). We therefore conclude that this last feature is the most critical one so far recognized for separating the Echimyidae and Octodontidae during the Deseadan, and hence refer *Sallamys* to the Echimyidae with some confidence. Lavocat recognized the similarity of the Deseadan echimyids and octodontids, and thought that "il s'agit pratiquement ici de saisir la séparation entre deux rameaux issus d'une même souche . . ." (1976: 72). He concluded (1976: 73) that there are many reasons for placing *Sallamys* in the Octodontidae; that it is by no means evident that the octodontids and echimyids were as clearly separable in the Oligocene as we had indicated (we think we made it clear in 1959, pages 300 and 389, that the Deseadan members of the two families were very closely related); and that he left *Sallamys* in the Echimyidae because Wood (1974b: 26) had so placed it and the evidence for shifting it to the Octodontidae was not conclusive. The two molar characters in which *Sallamys* agrees with the earlier octodontids (but also, it may be noted, with some Recent heteropsomyines) should no longer be considered as having diagnostic significance. As an aside, this is an argument against strict numerical taxonomy.

Hoffstetter and Lavocat (1970: 174) see a resemblance to *Paraphiomys* in the lower molars of *Sallamys*. This exists, but is completely offset by the wholly different dm_4 in *Paraphiomys pigotti* and *P. stromeri* (cf. Fig. 5D and Lavocat, 1973: Pl. 26, Figs. 7–10) as well as in the Fayum *P. simonsi* (Wood, 1968: Fig. 5F), transferred below (p. 520) to *Neosciuromys*. Furthermore, it must be noted that these species of *Paraphiomys*, like all the Petromuridae, have a cingulum anterior to the protoconid of the molars, a feature lacking in caviomorphs (see p. 496). As indicated below (p. 521), we retain *Paraphiomys* in the Petromuridae, rather than place it, as does Lavocat, in the Thryonomyidae.

Within the Echimyidae, *Sallamys* appears to fit rather comfortably into the Heteropsomyinae (Fig. 6), displaying, incipiently at least, a number of the molar characters of that group (Patterson and Pascual, 1968: 6). It differs from the Adelphomyinae in the more transverse lophs and lophids and a greater degree of unilateral hypsodonty, and from *Prospaniomys*, the earliest member of the Myocastorinae (if Patterson and Pascual were correct in deriving *Myocastor* from the *Spaniomys* group of echimyids), in the loss of the metalophids and the more complex dm_4 (cf. Fig. 5D,H).

In their definition of the Adelphomyinae, Patterson and Pascual (1968: 5) stated that there was "no unilateral hypsodonty." This is true of the later forms, but

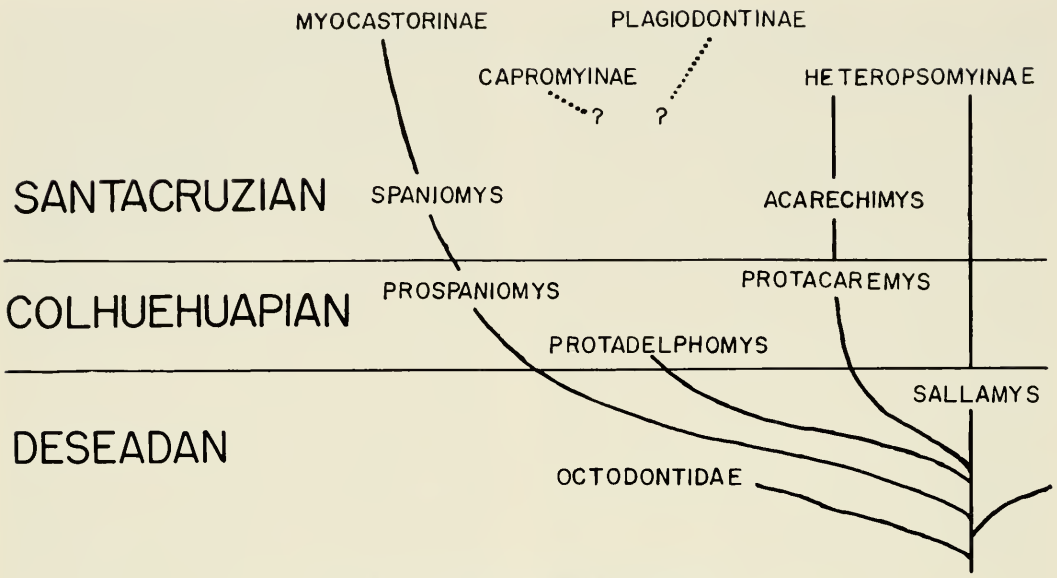

Figure 6. Phylogeny of the early Echimyidae.

the earliest, *Deseadomys*, shows some degree of it in the upper teeth. The statement should be amended to read: "slight initial unilateral hypsodonty, not subsequently increasing."

Sallamys displays no detectable tendencies toward the types of molar structure encountered in the Echimyinae and Dactylomyinae, subfamilies so far unrepresented, or at any rate unrecognized, in the Tertiary.

The Colhuehuapian *Paradelphomys* (Patterson and Pascual, 1968: Fig. 3) shows some resemblances to the dactylomyines in the obliquity of the lophids, the isolation of the posterolophid, the extension of the mesoflexid nearly to the anterior extremity of the tooth, and the simple trigonid of dm_4. Whether or not this is in any way indicative of affinity is at present quite uncertain and will remain so until later Tertiary dactylomyines are discovered. The possible relationships are suggested in Fig. 6.

On the basis of the few early forms then known, we tentatively sketched a phylogeny of the Echimyidae (1959: 302, Fig. 3) that suggested an early dichotomy into Adelphomyinae and the ancestry of the remainder of the family. The discovery of *Sallamys* suggests that this may have been an oversimplification, and that the actual situation was even more complex than we had supposed. *Sallamys* is about as advanced in molar structure as is *Deseadomys*, although in somewhat different ways, and is less advanced in the premolar. It is even more advanced over the later *Protacaremys* and *Prospaniomys* as regards crown height and metalophid reduction, and possesses a much more complex dm_4 than does *Prospaniomys* (cf. Fig. 5D,H). It is more advanced than the poorly known Colhuehuapian *Protadelphomys* in metalophid reduction and than *Paradelphomys* in lower milk molar complexity.

As pointed out below (p. 501), the adelphomyines and the *Spaniomys* group have a relatively simple dm_4, comparable to those of octodontids, whereas the known heteropsomyines have a complex dm_4 nearly comparable to that of *Cephalomys*. The latest Pleistocene or early Recent Antillean heteropsomyines have a simple dm_4, which suggests either that

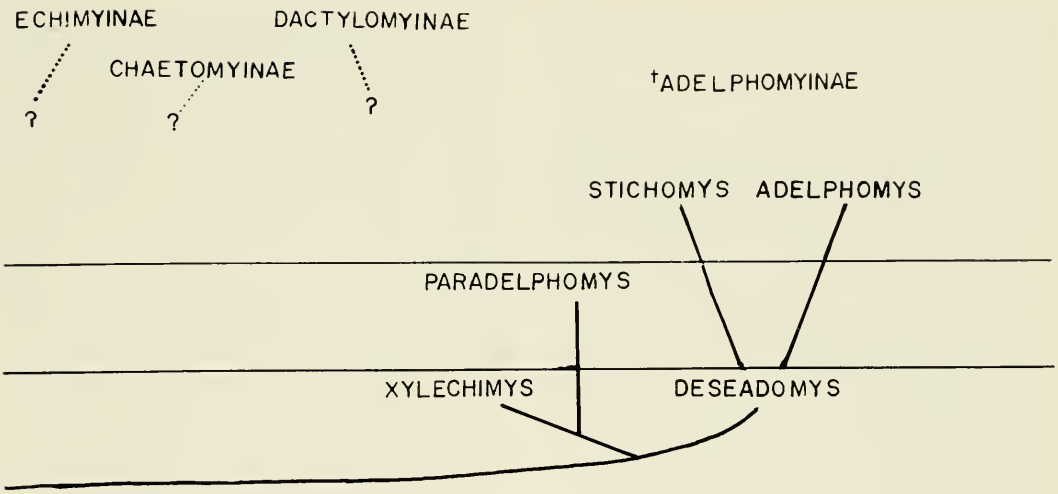

Figure 6. Continued.

not all early members of the subfamily had a complex one, or (a less probable hypothesis) that secondary simplification occurred in the ancestry of these forms.

We interpret these bits of evidence to mean that the heteropsomyines began their radiation at least as early as did the adelphomyines, and that the *Spaniomys* group may well be of equal antiquity and not an offshoot from the Heteropsomyinae, despite the close similarity between *Protacaremys* and *Prospaniomys* in molar structure.

Sallamys cannot have been ancestral to any Colhuehuapian or Santacruzian heteropsomyine now known. With a few easily made mental rearrangements of crests and valleys it would be possible to visualize it as being in or near the ancestry of various later forms, but in the absence of known intermediates such exercises would be vain and probably misleading. There is a resemblance, however, between *Sallamys* and *Chasichimys* of the Arroyo Chasicó (Pascual, 1967).

Due to conservative inertia as much as anything else, we have hitherto maintained the Capromyidae as a distinct family descended from the Echimyidae. Morphologically, this is not really justified, and, in general agreement with authors such as Ellerman (1940), we now place the two Antillean subfamilies Capromyinae and Plagiodontinae in the mainland family. Patterson and Pascual (1968:1, n. 2), in commenting on this possibility, stated that the subfamilies of the Echimyidae and Capromyidae would in that case become tribes. We do not take this step here because the capromyines and plagiodontines, while agreeing in possessing hypselodonty (the capromyine *Hexalobodon* alone excepted) and cement, differ in cheek tooth structure quite as much as do the other subfamilies. Their divergence, if they diverged from a common stock, may or may not have taken place in the Antilles; these subfamilies may or may not be relict survivors of the original caviomorph migration to South America (see below, p. 456); at present there is no evidence that bears on these questions.

The occurrence of macroscopic deposits of cement is sporadic in the Caviomorpha—as in rodents generally—and is

not necessarily indicative of higher affinities. In addition to the above-mentioned Antillean forms, it is present in the Deseadan *Litodontomys*, in its possible relative the Santacruzian *Olenopsis*, in chinchillids from the Deseadan on, in later eocardiines and in caviids and hydrochoerids, and in Pliocene and later octodontids, abrocomids, myocastorines and dinomyids. A thick deposit of cement is merely an enlargement of the universally present microscopic layer of cement that covers unerupted mammalian teeth, and is associated with hypsodonty and hypselodonty in rodent lineages in which the other components of the cheek teeth are either separated or only narrowly connected.

The peculiar genus *Chaetomys* is nowadays universally accorded a subfamily of its own, usually in the Erethizontidae. There have been few informed comments on the taxonomic position of this subfamily, due to the rarity of specimens of *Chaetomys*. Through the kindness of Dr. Paulo Emilio Vanzolini, one of us (B.P.) recently had the opportunity to examine a skeleton of *Chaetomys subspinosus* in the MZUSP.

If one looks mainly, or only, at the structure of the feet, placing the Chaetomyinae in the Erethizontidae is a logical step, the resemblance between the two groups in this respect being strikingly close. The cheek teeth of *Chaetomys*, however, are very different in structure from those of the erethizontids. On the basis of tooth structure, Schaub (*in* Stehlin and Schaub, 1951: 369) placed *Chaetomys* in the Echimyidae, following Miller and Gidley (1918: 445) who, however, as usual, gave no reasons for their action. Later (1958: 742), Schaub placed *Chaetomys* in the echimyid subfamily Echimyinae along with *Heteropsomys* and *Spaniomys*, as opposed to the only other subfamily he listed, the Dactylomyinae, again stressing the cheek-tooth structure.

This familial assignment is strongly supported by two characters that we regard as fundamental, both of them strongly negative as regards erethizontid affinities and one strongly positive as regards echimyid ones. In contrast to the known erethizontids and in agreement with all other living caviomorphs, *Chaetomys* lacks a posterior carotid foramen, and hence an internal carotid artery. Ellerman (1940: 175, Fig. 42) shows what could be interpreted as a small foramen anterointernal to the foramen lacerum posterior. In the MZUSP skull there is a depression in this area that does not communicate with the cranial cavity. Retention of this artery is a basic character of the New World porcupines, as Bugge (1974a: 71; 1974b: 70) has recently stressed. In agreement with all post-Deseadan echimyids and in contrast to all other caviomorphs, dm_4^4 are retained throughout life. There can be no doubt of this in the specimen of *C. subspinosus* examined (MZUSP unnumbered). The anterior cheek teeth are lower in crown height than are the first molars, and the flexi and flexids are more nearly obliterated, both features being due to wear. They were clearly the first of the series to have erupted, and X-rays have revealed no trace of replacing teeth beneath them. We believe reference of the Chaetomyinae to the Echimyidae to be fully justified.

With this transfer of *Chaetomys*, the Erethizontidae becomes a very compact group, and the Echimyidae an even more complex one. However, the Echimyidae now include all caviomorphs in which dm_4^4 are retained.

As a subfamily of the Echimyidae, the Chaetomyinae may be defined as follows: cheek teeth generally resembling those of the Echimyinae, but uppers with five lophs, metaloph forming an independent central crest; malar robust, very deep anteriorly, with large postorbital process nearly meeting well-developed postorbital process of frontal, and with little or no trace of jugal fossa on lateral surface; parietal crests well developed, only slightly convergent posteriorly; bulla with prominent porus acusticus exter-

nus directed anteroexternally; paroccipital process blunt, barely projecting; coronoid process of mandible greatly reduced; feet erethizontid-like.

Our present very tentative concept of echimyid phylogeny is summed up in Fig. 6. For so long as five of the eight subfamilies are unknown or unrecognized in the Tertiary, matters will remain in an unsatisfactory state; the evolution of all five may well have gone on for the most part in the northern half of the continent or (for the Capromyinae and Plagiodontinae) in the Antilles. Our placing of the Dactylomyinae next to the Adelphomyinae rests on nothing more than the few resemblances between the living forms and *Paradelphomys* noted above (p. 392); these hardly constitute compelling evidence. Whether or not the Echimyinae arose from or had a common ancestry with the Heteropsomyinae is wholly conjectural. The placement of the Capromyinae next to the Myocastorinae rests on somewhat firmer ground. The two groups have long been associated by a number of authorities, usually in a family of their own. George and Weir (1974: 102) conclude that on karyotypic evidence the two groups are closely related, more closely than either is to the heteropsomyine *Proechimys*, the only other echimyid whose karyotype was known to them. Woods (1972: 189) reported that myological evidence does not permit a decision as to whether *Myocastor* is an echimyid or an octodontid (dental evidence clearly favors echimyid affinities). Gorgas, in a comparative study of the rodent stomach and alimentary canal (1967: 367), has found that *Myocastor* and the capromyines stand apart from other echimyids—and also from each other—in some features. It seems to us that all this is not incompatible with an early origin of myocastorines from the basal echimyid stock, with the capromyines perhaps arising from some member of the myocastorine group. The position of the Chaetomyinae within the family is even more problematical than that of the other subfamilies.

Superfamily CAVIOIDEA Kraglievich 1930b

Series B. DASYPROCTIDAE, DINOMYIDAE and CUNICULIDAE (pp. 511, 523)

Family DASYPROCTIDAE Smith 1842

Incamys Hoffstetter and Lavocat 1970

Emended Diagnosis. Skull basically dasyproctid, with large orbits and bullae; snout elongate, ventral side horizontal; anterior part of fossa of origin for *M. masseter medialis* weakly marked, posterior part deep and corrugated; nasals parallel-sided, tubular anteriorly; large interpremaxillary foramen; incisive foramina enormous, elongate and laterally expanded; lateral wall of nasolacrimal canal very thin; interorbital fenestra between frontal and maxillary; anterior suture of malar with maxillary straight; no postorbital process or jugal fossa on malar; orbitosphenoid large, quadrate; no separate interparietal; mastoid continuous with bulla, inflated and septate; large fenestra between presphenoid and palatine, opening into orbitotemporal fossa; dental formula I_1^1 P_1^1 M_3^3, dm_1^2; incisors slender, proportionately small; cheek teeth tetralophate, marked lingual hypsodonty in uppers; anteroloph fully separate in earliest stages of wear, becoming joined with paracone buccally; other lophs unite early and converge posterointernally on hypocone; posterolophid isolated in early stages of wear of lower teeth; other lophids unite early and converge anteroexternally on protoconid; metalophid short, connected to protoconid.

Type Species. Incamys bolivianus Hoffstetter and Lavocat 1970.

Distribution. Deseadan Oligocene, Bolivia and Patagonia.

Incamys bolivianus Hoffstetter and Lavocat 1970

Figures 7–19

Incamys bolivianus Hoffstetter and Lavocat 1970: 173, Fig.; Lavocat, 1976: 50–54; Pl. 3, Figs. 1–7; Pl. 4, Figs. 1–3, 7.

Synonym. Incamys pretiosus Lavocat 1976: 54–59; Pl. 4, Figs. 4–6; Pl. 5, Figs. 6–7; Pl. 6, Figs. 3–5.

Diagnosis. As for the genus. Tooth measurements as given in Tables 3–4. The statistics seem to us to demonstrate that our sample represents a single variable species.

Type. Anterior portion of the skull, back as far as M^3, with associated left ramus, including a complete set of upper and lower cheek teeth, deposited in Muséum Nationale d'Histoire Naturelle, Paris; cited without identifying number by Hoffstetter and Lavocat (1970: 173) and without museum identification as SAL 117A (skull) and SAL 117B (ramus) by Lavocat (1976: 50).

Synonymized Species. Lavocat (1976: 54) described a second species of *Incamys, I. pretiosus,* which he differentiated from the genotypic species only by saying "molaires supérieures sans mésolophe, métalophe développé." If we are correct in not recognizing a mesoloph in any caviomorph, this becomes a meaningless distinction. Hoffstetter and Lavocat (1970: Fig.) and Lavocat (1976: Pl. 4, Figs. 1, 3) show the metaloph in *Incamys* either joined to (M^{1-3}) or about to join (P^4) the combined protoloph and mure. In only one (PU no. 20963, Fig. 17F) of the 50 specimens of upper cheek teeth in the Princeton collection does the metaloph do this, although in some other specimens it might make such a junction with further wear (Fig. 17D). Lavocat's specimens that he referred to *I. pretiosus* (1976: Pl. 4, Fig. 4; Pl. 6, Fig. 3) agree with the majority of our specimens. There is very considerable variability in all of the teeth of *I. bolivianus*, a point concurred in by Lavocat (1976: 46), enough so that we at first suspected the possibility of there being two species at Salla, but which we now feel means that there was only a single, highly variable species. Certainly the tooth measurements (Tables 3–4) indicate a high degree of size variability, but it seems to be continuous. It is partly due, as discussed below (p. 416), to the rotational eruption of the teeth, and there does not seem to be any association between size and morphological variants. Lavocat (1976: 41) suggests that there may have been a third species of *Incamys* at Salla, but he gives no data. Assuming that the scale given for Lavocat's stereophotos is accurate, the upper teeth of *I. pretiosus* (1976: Pl. 6, Fig. 3) fall within the size range of those of *I. bolivianus* (Table 3), and their pattern is identical to that here considered to be typical of *I. bolivianus* (Fig. 17B). We therefore conclude that *I. pretiosus* is a synonym of *I. bolivianus.*

Referred material. 140 specimens in the MNHN, Princeton, and MACN collections, listed in Appendix 1, p. 528.

A maxilla, SAL 118, containing RP^4–M^2, differs markedly from all other specimens that have been referred to *Incamys* (Lavocat, 1976: Pl. 4, Fig. 2), and represents, we believe, an undescribed genus, as discussed below (p. 430).

Horizon and Localities. Deseadan, early Oligocene, lower part of Estratos de Salla; Salla-Luribay Basin, Bolivia. PU nos. 20937–40 and 20945–6 are from Tomolo (see above, p. 383, for discussion of Tomolo and Toloma), midway between Salla and Aroma; nos. 20941–3 and 20947–9 were collected in the vicinity of Salla Farm; nos. 20950–2 are from dark red to reddish-brown rocks in the lower part of the Salla succession; nos. 20953–81 were found at Pampa Tapial, in a grayish-white, gypsiferous clay some 10 m above a 30–50 cm thick bed of greenish-gray limestone within an area of 20 by 20 m that also yielded specimens of *Sallamys pascuali.* Nos. 20916–36 and 20949 are without precise locality data. The partial skull, PU no. 20944, was found at locality "V-33," the precise location of which is not known to us (L. Braniša, field notes). MACN no. A 52-113 is presumably from Cabeza Blanca, Chubut, Argentina.

Description. The juvenile Princeton skull has suffered some distortion—partially corrected in the figures—and was enclosed in exceedingly hard matrix,

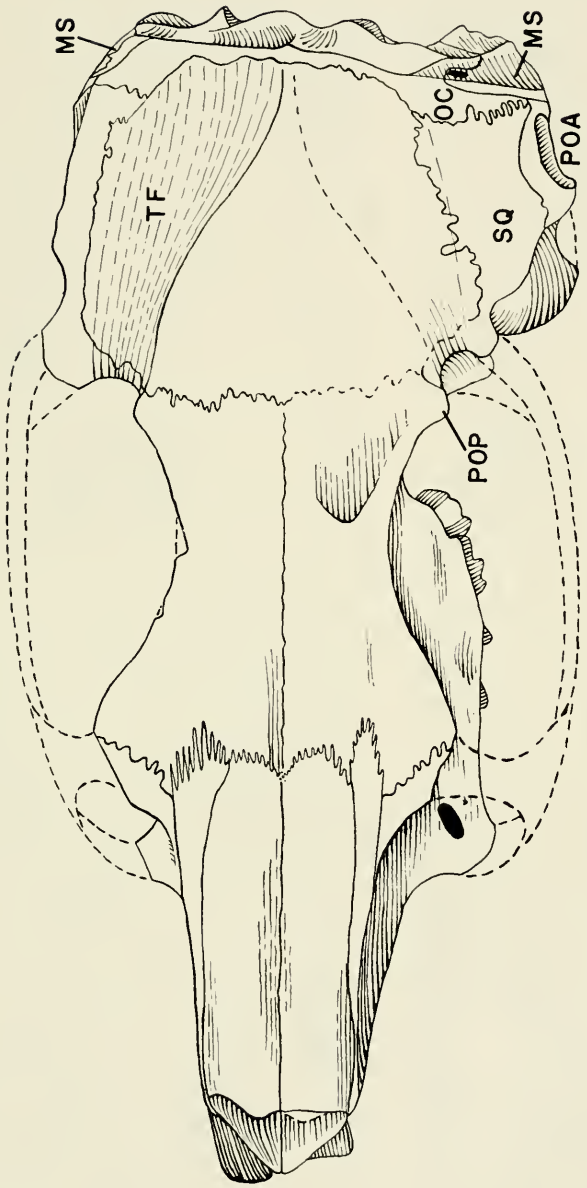

Figure 7. Dorsal view of the skull of *Incamys bolivianus*, PU no. 21726, juvenile, ×3.

Abbreviations: MS—mastoid; OC—occipital; POA—porus acusticus externus; POP—postorbital process; SQ—squamosal; TF—temporal fossa.

which unfortunately tended to be at its hardest along suture lines and around foramina. Removal of all of the matrix has not been possible, with the result that some details are still obscure. The skull of PU no. 21945, however, was in a softer matrix, was less distorted, and has provided an almost complete understanding of the skull structure. Moreover, the facial region (PU no. 20944) supplements the skulls in various features. These three specimens differ somewhat in size, the facial region representing the largest individual. These differences seem to be due to age. The skull of PU no. 21726 is that of an immature animal in which the milk molars are still in place and M^3 has just come into wear. Series of living dasyproctids reveal that skull growth continues until the full adult dentition is in use.

The skull as a whole is strongly arched, agreeing in this with the type (Lavocat, 1976: 57), and is about as in *Myoprocta*, with large orbits and very large bullae. The region in front of the cheek teeth forms approximately a quarter and the region posterior to the front margin of the glenoid cavity approximately a third of the total length (Figs. 10, 12, 14). The skull roof is much flatter transversely than in later dasyproctids, in this respect resembling *Cephalomys*, and is even slightly concave in the nasal and frontal regions. In contrast to other members of the family, there is a marked interorbital narrowing of the dorsal surface of the skull, and the braincase is flatter and relatively wider than in later dasyproctids. The sagittal crest is short and feebly expressed (Figs. 7–8).

The rostrum is moderately long and rather slender, comparable to the rostra of living dasyproctids in general proportions, but less tapering and more nearly parallel-sided, so that the dorsal root of the zygoma stands out about at right angles to the sides of the rostrum (Fig. 8), a resemblance to *Cephalomys*. The ventral profile of the snout is nearly straight, as in living dasyproctids, and there is a suggestion of the characteristic abrupt downturn of the premaxilla immediately behind the incisors (Fig. 10).

The infraorbital foramen is preserved *in toto* only on the right side of PU no. 21945. The foramen was a large, vertically oriented oval, rather different from those of the modern dasyproctids. Because both the dorsal and ventral roots of the lateral wall of the foramen are considerably elongate anteroposteriorly in contrast to the slender central section of the lateral wall, the infraorbital foramen is nearly circular as seen from the side (Fig. 12). The dorsal and ventral roots extend about equally far forward, so that the dorsoventral axis of the foramen would have been vertical, rather than inclined forward as Lavocat believed (1976: 52). There is a prominent elevation (below the ridge that marks the course of the incisor) that occupies part of the ventral border of the masseteric fossa. A similar elevation occurs in living dasyproctids, but not in *Neoreomys*.

The nasals, not preserved in either of Lavocat's partial skulls, are very much longer than in *Dasyprocta* or *Myoprocta*. They extend back to a point above dm^4 in the juvenile or M^1 in the adult, and slightly behind the lacrimal foramen, about as in *Cephalomys* and *Neoreomys*, although their posterior ends are in front of the lacrimal foramen in the Santacruzian genus. Very long nasals are characteristic of the Paramyidae and Reithroparamyidae (Wood, 1962a: Figs. 2A, 13A, 48A) and we accordingly interpret the condition in *Incamys* (and also in *Branisamys*, see below, p. 433) as primitive. *Platypittamys* has somewhat shorter nasals, while those of living dasyproctids are shorter still. The anterior end of each nasal is tubular, the tubular part forming perhaps half the length of the bone. In living dasyproctids, the combined nasals have a tubular anterior end, but there is no groove between the bones as there is in *Incamys* (Figs. 7–9). The nasals of *Neoreomys* are much less tubular than in

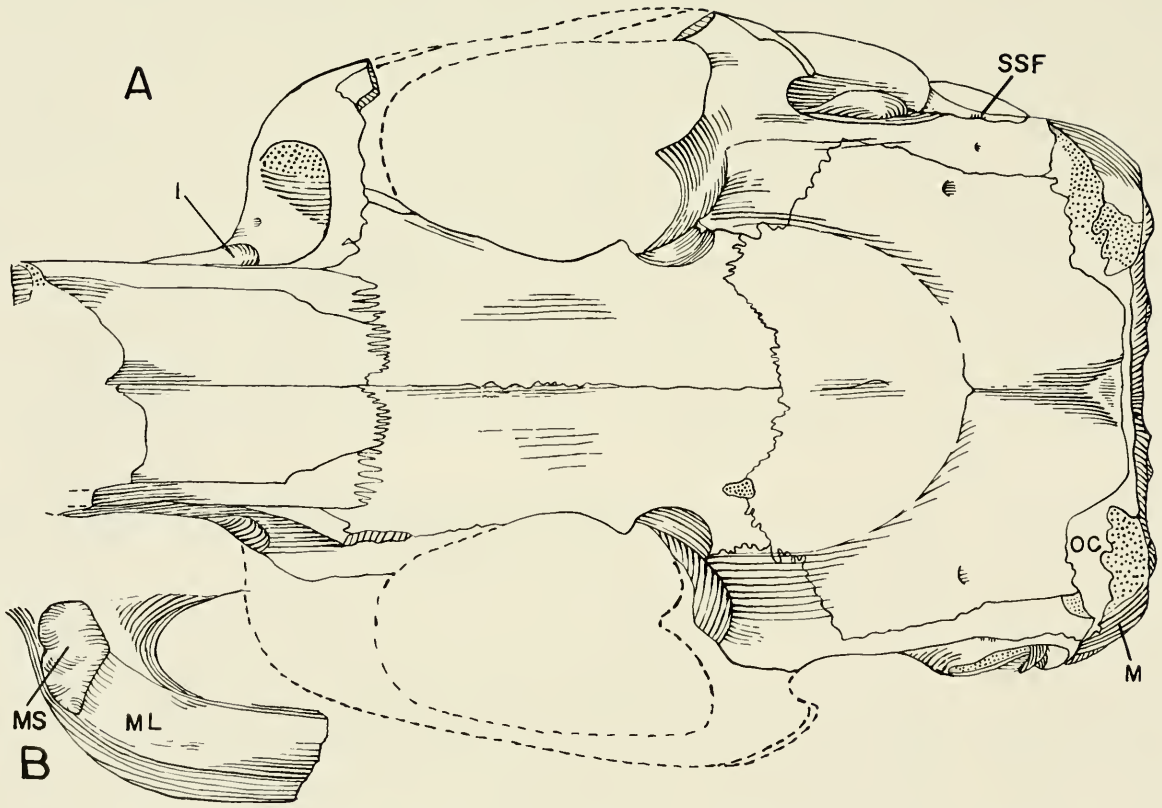

Figure 8. *Incamys bolivianus*, PU no. 21945. A. Dorsal view of skull, ×3. B. Ventral view of anterior part of right zygoma, anterior end to the right. ×5.

Abbreviations: I—base of upper incisor; M—mastoid; ML—fossa for origin of *M. masseter lateralis*; MS—fossa for origin of *M. masseter superficialis*; OC—lateral process of occipital; SSF—subsquamosal foramen.

living dasyproctids. The posterior portions of the nasals in *Incamys* are flattened, even slightly concave transversely. The sides of the bones are nearly parallel, but they are slightly pinched at the middle. The nasals are generally similar in outline to those of modern dasyproctids. The nasofrontal suture bends forward toward the midline, an irregularly pointed process of the frontals separating the posterior ends of the nasals (Figs. 7–9).

The ascending portions of the premaxillaries are long and somewhat expanded at their posterior ends. Their terminations are curiously asymmetrical in two of the three specimens at hand (Figs. 7–9). On both sides of PU no. 21726 they extend back farther than the nasals, whereas only the right one of PU no. 20944 does so. The left premaxillary of the former is of normal shape, but the right in the course of development evidently expanded medially at the expense of the nasal, reaching farther toward the midline and taking over the area occupied on the left side by a small, forwardly extending wedge of frontal. The nasals and premaxillae reach back to the same level in PU no. 21945, and the two premaxillae are symmetrical (Fig. 8A). The fronto-maxillary suture is well in advance of the rear of the nasal and premaxillary, and is not so obliquely inclined as in living dasyproctids and *Cephalomys*. In *Neoreomys* the entire anterior end of the frontal is an essentially transverse line. On the ventral side of the bones, the interpremaxillary foramen is very large in PU no. 20944, much larger than in any other dasyproctid we have seen, being about 1.6 mm in diameter (Fig. 14B); it is relatively smaller, although still large, in the type (Lavocat, 1976: Pl. 3, Fig. 2) and in PU no. 20953, both of which are smaller and younger individuals, and this area is missing in PU no. 21945. It is partially obscured by crushing in PU no. 21726. The size of the foramen is variable in Recent dasyproctids.

On the lateral side, the premaxillary part of the fossa for the origin of *M. masseter medialis, pars anterior* is not so clearly defined as in *Neoreomys* and living dasyproctids, and does not have so large an anterior extension (Fig. 10A), although it is relatively deep dorsoventrally. Lavocat (1976: 51) apparently confused the crest marking the anterior limit of the masseteric fossa (Fig. 10A; AM) with the premaxillary-maxillary suture on the ventral lateral part of the snout. His description of the suture, "elle part de façon rectiligne à 45 degrés vers le haut et l'avant," agrees perfectly with the limits of the masseteric fossa as we indicate them on Figs. 10A and 12, and is very unlike the highly crenulate suture that we show on the same figures. A close examination of Lavocat's excellent stereophoto (1976: Pl. 3, Fig. 1) shows that the suture in this area is still covered by a thin layer of matrix.

A striking feature of the *Incamys* skull is the enormous size of the incisive foramen, which occupies the greater part of the palate anterior to the cheek teeth (Fig. 14A,B). The anterior part of this aperture seems to correspond to the normal rodent incisive foramina, but the posterior part is peculiar indeed. The anterior half of the septum between the foramina is broad and rounded and reaches the level of the palate in the usual manner, but the posterior half is a slender vertical septum that does not reach so far ventrad (Fig. 14B). The premaxillary-maxillary suture reaches the sides of the foramina near the level at which the change in the septum occurs. The apparent difference between the shape of the suture in PU no. 21726 (Fig. 14A) and that in the type (Lavocat, 1976: Pl. 3, Fig. 2) is merely because this area had not been cleared of matrix in the latter. Near the rear of the opening, the ventral margin of the septum is about 3 mm dorsal to the palate (Fig. 14B). None of the available specimens is complete, but by combining them all (Fig. 14A; Lavocat, 1976: Pl. 3,

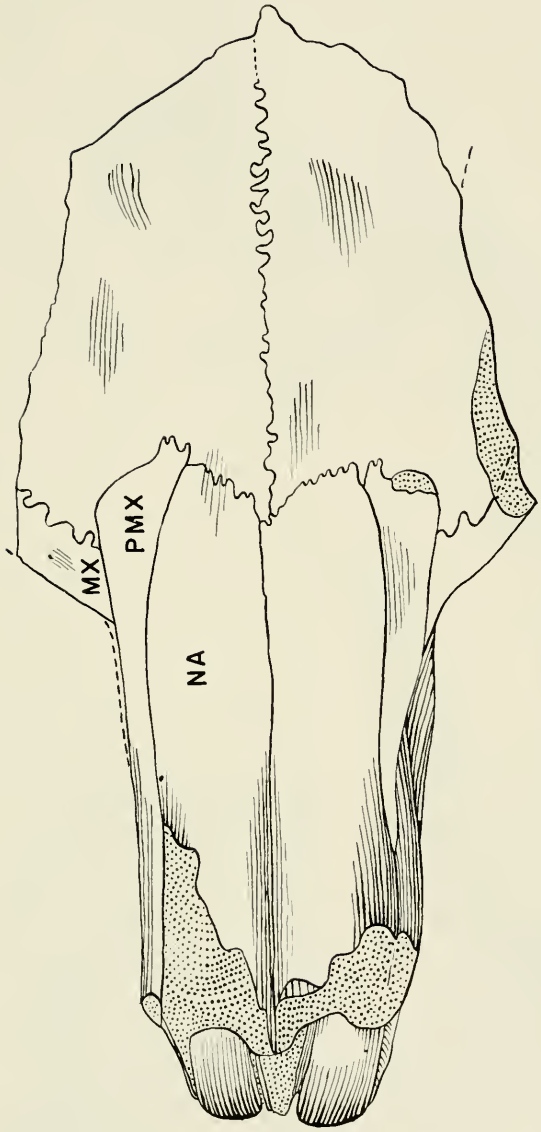

Figure 9. Dorsal view of partial skull of *Incamys bolivianus*, PU no. 20944, ×4.
Abbreviations: MX—ascending process of maxillary; NA—nasal; PMX—premaxilla. Dotted areas are matrix.

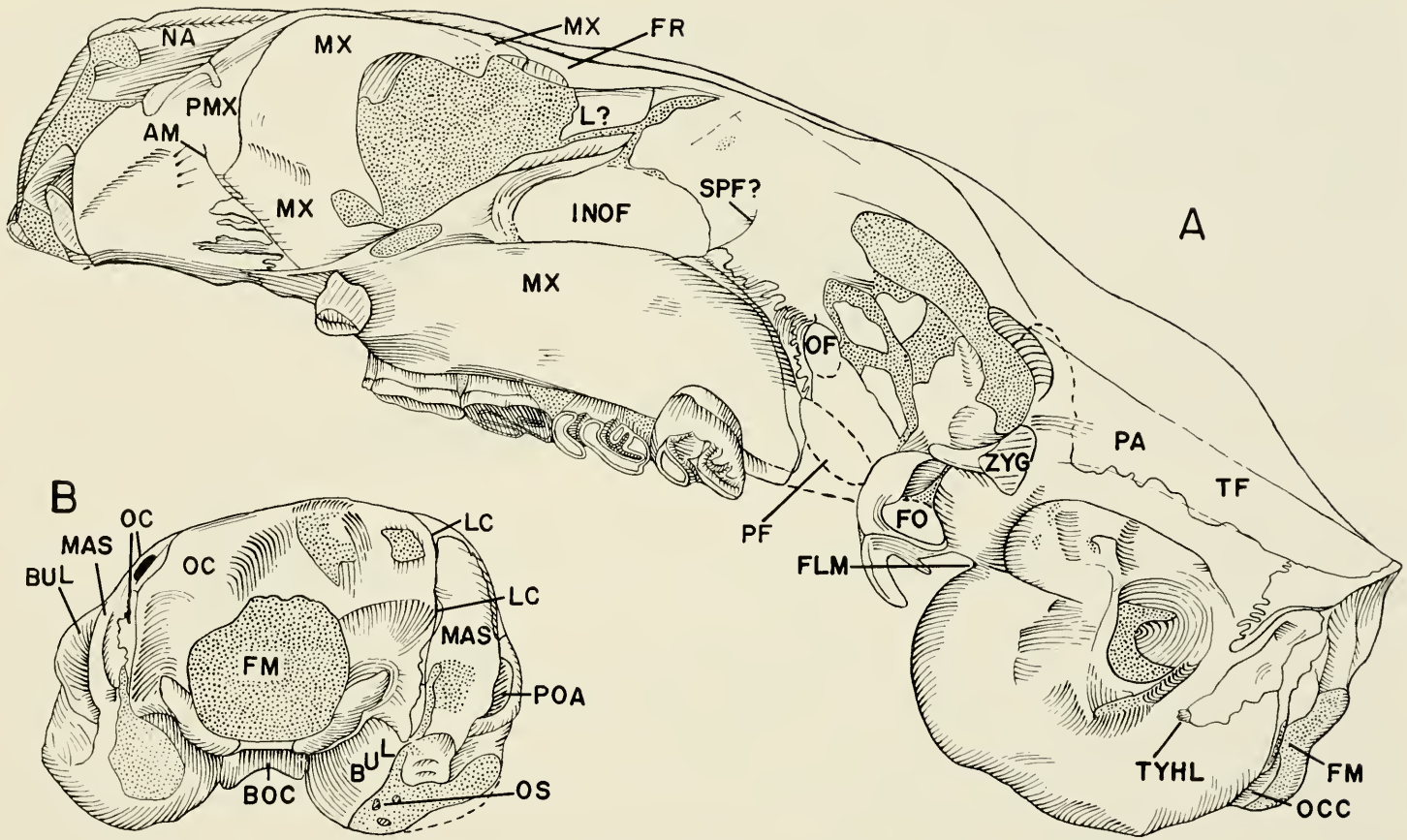

Figure 10. Skull of *Incamys bolivianus*, PU no. 21726, juvenile. Dotted areas are matrix. A. Lateral view, ×4. B. Occiput, ×3.

Abbreviations: AM—anterior limit of masseteric fossa; BOC—basioccipital; BUL—bulla; FLM—foramen lacerum medium; FM—foramen magnum; FO—foramen ovale; FR—frontal; INOF—interorbital fenestra; L?—possibly lacrimal; LC—lambdoid crest; MAS—mastoid; MX—maxillary; NA—nasal; OC—occipital; OCC—occipital condyle; OF—optic foramen; OS—??auditory ossicles; PA—parietal; PF—pterygoid fenestra; PMX—premaxillary; POA—porus acusticus externus; SPF—?sphenopalatine foramen; TF—temporal fossa; TYHL—area of articulation of tympanohyal; ZYG—broken base of zygoma.

Fig. 2) it is clear that, in life, the septum was continuous, as postulated by Lavocat (1976: 51). The maximum width, across both foramina and the septum, is 5.0 mm or perhaps a little more. There is no trace of the premaxillary-maxillary suture on the septum between the incisive foramina in any of the specimens, although in all of them a median suture is discernible. We therefore suspect that all or most of the septum may be composed of the premaxillaries, as in other caviomorphs. Just behind the premaxillary-maxillary suture, on the lateral wall of the fenestra, is what seems to be a large opening, probably the anterior end of the nasolacrimal canal. The incisive foramina are closed posteriorly slightly behind the base of the upper incisors and opposite the middle of P^4, at which point the septum descends abruptly to the ventral margin of the opening.

We have not observed similar fenestrae in any living dasyproctid, in all of which the premaxillary-maxillary suture passes across the palate at the rear of the incisive foramina. However, in known fossil dasyproctids there appears to be a backward expansion of the foramina into the maxillary (*Cephalomys*, Wood and Patterson, 1959: Figs. 21B, 22B; *Neoreomys*, Scott, 1905: Pl. 65, Fig. 1; *Scleromys*, Scott, 1905: Pl. 65, Fig. 13). In *Neoreomys* (PU no. 15572), the suture crosses the middle of the foramina, the posterior part of the foramina being solidly roofed by the maxillae. A posterior enlargement of the incisive foramina is clearly visible in the Santacruzian octodontids *Sciamys* (Scott, 1905: Pl. 67, Figs. 1f, 5a, 6a, 7a) and *Acaremys* (Scott, 1905: Pl. 67, Fig. 4a), and echimyids (Scott, 1905: Pl. 67, Fig. 10a), and also occurs in Recent members of these families and in *Abrocoma*, *Chinchilla* and *Lagidium*. This may be a primitive character for caviomorphs. The octodontids *are* primitive caviomorphs, and it should be noted that the enlargement is present in the North American Uintan franimorph *Protoptychus* (Wahlert, 1973). No trace of an enlargement is present in the Deseadan dinomyid *Branisamys* (possibly indicating an early reduction in the size of the opening in this family); and the two skulls of the primitive caviomorph *Platypittamys* are so preserved as effectually to conceal this area. This region is not preserved in the partial skull of *Sallamys* (Lavocat, 1976: Pl. 2, Figs. 1, 4). The foramina are very short in the snout described by Lavocat as *Luribayomys masticator* (1976: Pl. 5, Fig. 1).

An elongate incisive foramen, apparently extending as far back as the level of the anterior end of the cheek teeth, was present in the early Oligocene African *Metaphiomys* (Wood, 1968: Fig. 6A), where its development was apparently similar to that in *Petromus* (Tullberg, 1899: Pl. 6, Fig. 16). In these forms, however, the incisive foramina are sunk into a palatal depression (Wood, 1968: 51–52) quite different from conditions in most caviomorphs, although there are some similarities to the well-developed gutter that leads back from the foramina in *Neoreomys* (PU no. 15572). The foramen in the African forms is more normal in its shape than in *Incamys* and the Santacruzian octodonts. Such an enlarged incisive foramen is not primitive for rodents (e.g., Wood, 1962a: Figs. 13C, 24C, 48B for paramyids and reithroparamyids; Dawson, 1961: Pls. 2, 3 for *Sciuravus*).

The fossa for the origin of *M. buccinator* extends forward, lateral to the incisive foramina, as far as the premaxillary-maxillary suture, approximately as in *Cephalomys*, *Neoreomys* and *Scleromys*. We disagree with Lavocat's statement (1976: 52) that this fossa is quite different from what is found in other caviomorphs. In living dasyproctids the fossa extends medially almost to the midventral line in adult specimens, the fossae of the two sides being separated only by a narrow ridge. It would seem that the buccinator is a more powerful muscle in *Dasyprocta* and *Myoprocta* than it was in known ear-

lier genera. This suggests the possibility that in the ancestry of these forms the posterior part of the incisive foramina may have become floored by medial extensions of the maxillae that enlarged *pari passu* with the increase in the size and strength of the buccinator muscle in later members of the family.

In the living forms, and even more in *Neoreomys*, the maxillary part of the fossa for *M. masseter medialis, pars anterior,* dorsal to the incisor, is the deepest part. This deepening is present to an exaggerated degree in *Incamys*, where the area seems to be subdivided into a number of subsidiary pockets (Fig. 10). However, the absence of these from both sides of the best preserved skull (Fig. 12) suggests that they may have been formed post-mortem either by crushing or by breaking. The right zygoma is preserved in PU no. 21945, revealing a fossa for the origin of *M. masseter superficialis*, distinct from that of *M. masseter lateralis* (Fig. 8B).

There is a large opening in the maxillary on the dorsal surface of the ventral root of the zygoma (Fig. 7). This, we believe, is too far laterad to be related to the nasolacrimal canal, and we interpret it as a nutritive foramen for the superior alveolar blood vessels (cf. Wood, 1974a: 35). Lavocat (1976: 54) mentioned "un petit foramen qui est sans doute l'entrée du nerf alvéolaire antéro-supérieur." This foramen is faintly visible in his Pl. 3, Fig. 1, where it can be seen to be as large as in the Princeton material.

The orbital portion of the maxillary is arched transversely over the roots of the cheek teeth and does not meet the orbital portion of the frontals above the molars. In PU no. 21726 (Fig. 10A) there is an oval vacuity here in which no trace of bone was present, and in the older PU nos. 20944 (Fig. 11) and 21945 (Figs. 12, 15A) there are corresponding but somewhat smaller openings. Such an opening is likewise present in the type (Lavocat, 1976: Pl. 3, Fig. 1). This is a puzzling feature that seems to have resulted either from a lack of ossification in the ventral part of the frontal or, less probably, from universal post-mortem loss of delicate bone. In living dasyproctids the ventral portion of the frontal is very thin and grows down over the maxillary; union of the two bones is not entirely complete in some of the younger individuals at hand, and in these it is possible to pass a bristle through the skull between the frontal and the maxillary. Since the parts of the frontals bordering these vacuities in the fossils do not show signs of breakage, and since the openings are present in all four specimens (the type skull of *I. pretiosus* would seem, from Lavocat's stereophotos, not to have had this area cleared of matrix), we conclude that the vacuities are natural. We have termed the opening the interorbital fenestra (Figs. 10, 12, 15A; INOF). Lavocat (1976: 52 and Fig. 3; I) identified this opening as the sphenopalatine foramen, an interpretation that seems highly improbable to us, although the foramen possibly is included in the fenestra. What we have identified as the foramen (Fig. 10; SPF) lies farther to the rear. Openings of this nature within the orbit are highly unusual among rodents, but they do occur (e.g., *Myosciurus*, *Jaculus*; Ellerman 1940: Figs. 91, 158).

The palatal portions of the maxillary send a sharply pointed median process forward into the posterior part of the enormous incisive foramina. This and the equally pointed anterior end of the palatines are situated dorsal to the level of the adjacent cheek teeth, and form the roof of a prominent groove that extends from the incisive foramina to the middle of M^1 (Fig. 14A), and ends at the posterior palatine foramina.

The frontals are suturally separated for most of their length as seems generally to be true of caviomorphs, franimorphs, and paramyids (Wood, 1962a: Figs. 13A, 31A, 35A, 41A, 48A, 57A). The same is true of Old World hystricognaths. In PU

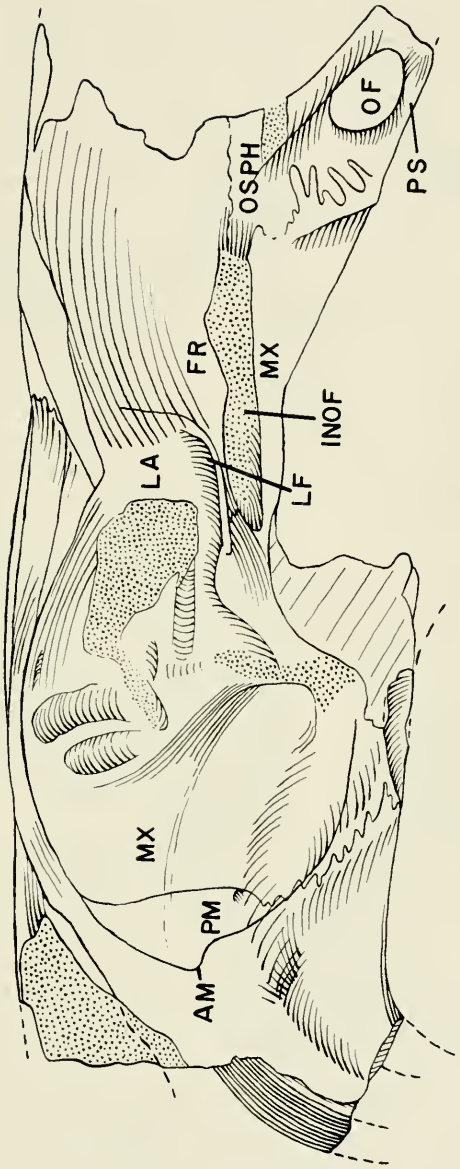

Figure 11. Partial skull of *Incamys bolivianus*, PU no. 20944, lateral view, ×4.

Abbreviations: AM—anterior limit of masseteric fossa; FR—frontal; INOF—interorbital fenestra; LA—lacrimal; LF—lacrimal foramen; MX—maxillary; OF—optic foramen; OSPH—orbitosphenoid; PM—premaxillary; PS—presphenoid. Dotted areas are matrix.

no. 21945 (Fig. 8A), the suture extends the entire length of the bones, as in *Myoprocta* and *Dasyprocta*. The dorsal surface is extremely flat, with slight longitudinal depressions on either side of the midline (Fig. 8A), as in *Neoreomys*. As noted above, the frontals narrow at the middle of the orbits. Within the orbit, the frontal is well preserved only in PU no. 21945 (Figs. 12, 15A). It was nearly as concave as in living dasyproctids. The orbital process of the frontal is essentially rectangular (Fig. 15A). The vertical lacrimo-frontal suture is hidden in Figure 12 by the lateral wall of the infraorbital foramen. At the posterior end, the frontal-squamosal suture is highly crenulate, but is also nearly vertical. Ventrally, the posterior three-fifths of the frontal meets the orbitosphenoid in a line that is generally straight but irregular in detail (Fig. 15A). The anterior part of the ventral border of the frontal is formed by the interorbital fenestra.

There is a small but pointed postorbital process of the frontal, somewhat behind the middle of the orbit (Figs. 8, 12), that extends out over the fossa for *M. temporalis*, as in *Dasyprocta* and *Myoprocta*. Behind this, and in the squamosal immediately behind the frontal-squamosal suture, is a smaller, rounded postorbital process. Between these two processes, an anterior slip of *M. temporalis* apparently extended a short distance onto the dorsum of the skull, arising entirely from the frontal (Fig. 8). There is no trace of the posterior postorbital process, or of any division of *M. temporalis*, in the skulls of *Neoreomys*, *Dasyprocta*, or *Myoprocta*. A similar condition, however, may be seen in the skull of *Myocastor* (Ellerman, 1940: Fig. 20). *M. temporalis* in caviomorphs is divisible into three portions which may be called the main, orbital and posterior parts (Woods, 1972: 129–130). The main part arises from the temporal fossa on the dorsum of the skull; the orbital from the frontal and squamosal within the orbit; and the posterior from the squamosal root of the zygoma (*op. cit.*). It would seem, therefore, that the orbital portion of *M. temporalis* must have been unusually large and distinct in *Incamys*, as would also seem to be the case in *Echimys* (Tullberg, 1899: Pl. 8, Figs. 7–8) and in *Proechimys* (Woods, 1972: Fig. 2A,B). It is possible that this is a primitive condition for caviomorphs. In the franimorphs, no skulls are preserved so as to show whether or not the orbital part of *M. temporalis* was visibly distinct on the dorsal surface. However, in *Paramys* (Wood, 1962a: 17; Figs. 2A,B; 13A,B), *Thisbemys* (*op. cit.*: Fig. 36A), and manitshines (*Pseudotomus*, *op. cit.*: 174; *Ischyrotomus*, *op. cit.*: 190; Figs. 68A,C; 71B,C; *Manitsha*, *op. cit.*: 222), the conditions are basically similar to those in *Incamys* except that, in this last genus, the fossa for the orbital part of *M. temporalis* is in the frontal; in the paramyids, it is in the alisphenoid or parietal. Among the thryonomyoids, there is possibly a rather similar situation in *Paraphiomys stromeri* (Lavocat, 1973: Pl. 2, Figs. 3–4; the specimen was not prepared enough for us to feel at all certain), and *Diamantomys luederitzi* (Lavocat, 1973: Pl. 3, Figs. 1–2), but rather clearly not in *Paraphiomys pigotti* (*op. cit.*: Pl. 1, Figs. 3–4) and apparently not in *Thryonomys* or *Petromus*.

The right lacrimal is partly preserved in PU nos. 20944 (Fig. 11) and 21945 (Fig. 12). There was a small expanse of the bone on the dorsum of the skull (Fig. 8) and it forms the posterior part of the dorsal root of the zygoma as in living dasyproctids and in *Neoreomys*. It is uncertain, due to breakage, just how far down the zygoma the bone extended. It may have reached the malar, as it does in *Neoreomys*. The opening of the nasolacrimal canal is near the posteroventral border of the bone. The canal curved forward and slightly ventrad. In *Neoreomys*, the opening of the canal is farther forward, on the lateral buttress of the lacrimal. In the living Dasyproctidae, the canal leads

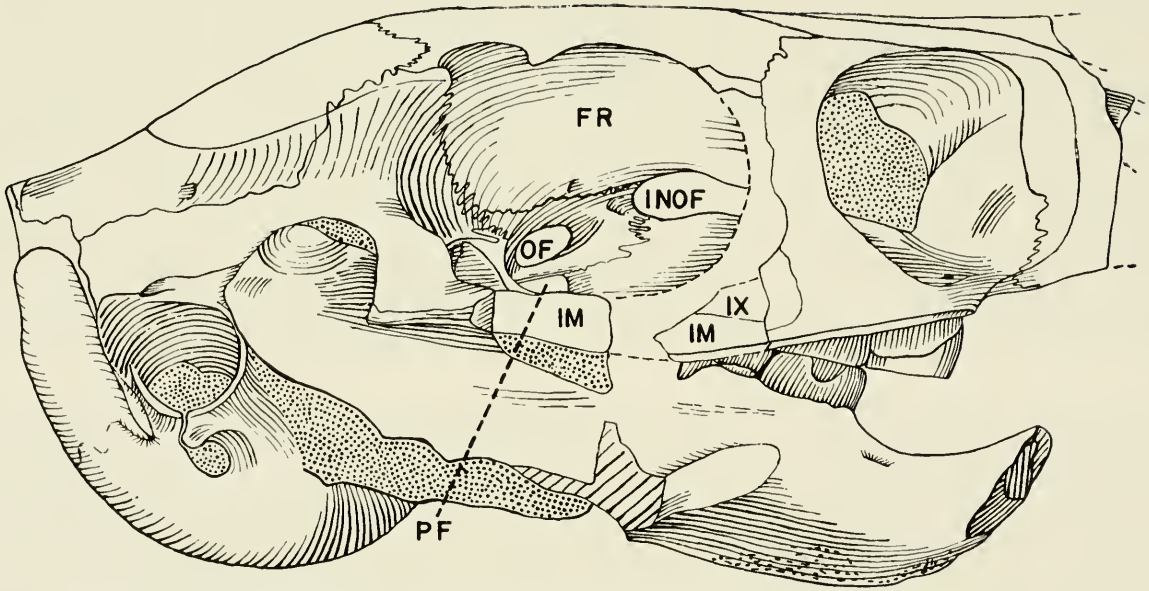

Figure 12. *Incamys bolivianus,* PU no. 21945, right lateral view of skull, ×3. Partly restored from left side.

Abbreviations: FR—frontal; IM—imprint of medial face of malar; INOF—interorbital fenestra; IX—imprint of medial face of maxillary; OF—optic foramen; PF—pterygoid fenestra.

forward and downward from the lacrimal foramen to the nasal passage, in a normal manner. However, half of its length is exposed by a large, oval opening in the medial wall of the masseteric fossa. There is a large opening in this position in *Neoreomys* (Scott, 1905: Pl. 64, Fig. 6), but not, apparently, in *Cephalomys* (Wood and Patterson, 1959: Fig. 21C). As preserved in *Incamys*, the course of the canal is a deep groove extending from the lacrimal foramen nearly as far as the rear of the upper incisor. Presumably, as also indicated by Lavocat (1976: 52), there was a thin lateral wall covering most of this groove, although there may have been an opening in it just behind the incisor. However, the preservation is such that we could not be certain whether or not the lateral wall was originally present in *Incamys*, or how large the supposed lateral opening might have been. The anterior limits of the lacrimal could not be determined because all specimens were broken in this area, but we find it impossible to visualize any construction of the lacrimal that would not have included a laterally directed buttress near its anterior end, supporting the dorsal root of the zygoma, a structure that is very characteristic of fossil and Recent dasyproctids, and that is also present in caviids and *Hydrochoerus*.

Small portions of both ends of the malar and the imprint of the medial surface of most of the remainder are preserved in PU no. 21945 (Fig. 12; IM). The ventral surface of the arch is uniformly rounded, as in *Myoprocta* and *Dasyprocta*. There is no suggestion of the pronounced ventral angulation seen in *Paraphiomys* (Lavocat, 1973: Pl. 1, Fig. 4). The anterior end of the bone is very similar to that of *Myoprocta*—much more so than like *Dasyprocta*. The malar forms a thin plate that lies on the lateral surface of the maxilla, which is exposed on the lateral side ventral to this thin plate. The imprint of the medial face of the zygoma shows the malar-maxillary contact rising posterodorsally across the arch. The preserved anterior portion of the malar is restricted to the horizontal bar of the zygoma, and does not extend far up the plate lateral to the infraorbital foramen, in this resembling both *Myoprocta* and *Dasyprocta*. How high it extended on the arch and whether or not it reached the lacrimal are undeterminable. The anterior malar-maxillary suture is slightly irregular, but not crenulate, and forms almost a straight line. The slender posterior tip of the malar extends a short distance behind the posterior end of the zygomatic process of the squamosal, as in *Myoprocta* and *Dasyprocta*. It is, however, more exposed in lateral view (Fig. 12) than in those genera.

The central part of the malar is missing. The imprint in the matrix preserves almost the entire ventral limit of the arch, and seems to preserve at least half of the dorsal limit. It is possible that part of the dorsal imprint has been broken away, although there is no evidence that it has. If the imprint of the central part of the malar is as complete as it seems to be, the bone was of essentially uniform dorsoventral diameter for its entire length, resembling *Myoprocta* and *Dasyprocta* in this, but perhaps being a little less enlarged anteriorly. There is absolutely no similarity in any respect to the malar of *Paraphiomys* (Lavocat, 1973: Pl. 1, Fig. 4; Pl. 2, Fig. 4) or *Diamantomys* (*op. cit.*: Pl. 3, Fig. 2), both of which form heavy vertical plates.

The fused palatines extend forward to the middle of P^4 or dm^4, as in *Dasyprocta*. Lavocat (1976: 52) stated that the maxillary-palatine suture reaches the level of the posterior end of P^4. A careful examination of his stereophoto (*op. cit.*: Pl. 3, Fig. 1) suggests that, if this area had been completely prepared, the suture would probably have the position shown in our Fig. 14A. The maxillary-palatine sutures diverge posteriorly, at first abruptly, then very gently, and then abruptly again behind M^3. The posterior palatine foramina

are completely enclosed by the palatines. On the midline, the palate ends opposite the middle of M^2 (Fig. 14A) as in *Cephalomys*. Lavocat (1976: 54) suggests that there may have been a rudimentary median process at the midline of the posterior margin of the palate of the type (1976: Pl. 3, Fig. 2); one clearly was absent in PU no. 21945 and in the slightly younger PU no. 21726 (Fig. 14A). The palatine forms the lateral walls of the pharyngeal passage behind the rear of the hard palate, reaching almost to the front of the pterygoid fossa (Fig. 15B), about as in *Reithroparamys* (Wood, 1962a: Fig. 41B), the only franimorph in which any of this area is known. The palatine-pterygoid suture is highly crenulate. In both of these respects, *Incamys* is very similar to *Dasyprocta* and *Myoprocta*.

In PU no. 21945, the palatine-pterygoid suture very clearly lies behind the middle of the "orifice choano-orbitaire" (choano-orbital fenestra), as stated by Lavocat, and as shown in Fig. 15B, but there is what might be another suture along the lateral wall of the pharyngeal passage anterior to this (Fig. 15B; ?). It is very doubtful that this really is a suture; irregularities in this area that are vaguely suture-like can be seen in some individuals of *Dasyprocta*. The orbital process of the palatine extends along the front of the choano-orbital fenestra up to the orbitosphenoid (Fig. 15A). We do not know whether this fenestra has any great significance or not. A similar opening is present in many sciurids, but absent in others, varying from present to absent within the genus *Sciurus*.

The orbitosphenoid is a large bone. Its dorsal margin is somewhat higher than the dorsal limit of the alisphenoid, and it separates that bone from the frontal (Fig. 15A). The suture between the orbitosphenoid and the maxillary is irregular, especially in its anterior portion, just beneath the rear of the interorbital fenestra (Fig. 15A). After a short, generally vertical contact, the suture turns backward nearly horizontally, the anterior portion of the orbitosphenoid lying dorsal to the maxillary. Below the posterior portion of the bone is the orbital opening of the choano-orbital fenestra (Fig. 15A), that opens both into the pharyngeal passage between the pterygoid and the presphenoid, and also into the pterygoid fossa. The confluent optic foramina are entirely within the orbitosphenoid. The bone forms the median wall of the foramen lacerum anterius (Fig. 15A).

The pterygoid forms the anterior end of the pterygoid fossa and its median wall (Fig. 15B). The internal pterygoid process, preserved *in toto* only on the right side of PU no. 21945, is a long, slender process, reaching back to touch the anteromesial tip of the bulla (Fig. 15B), as in the living dasyproctids. It is bounded dorsally by the usual vacuity between it and the bulla.

The alisphenoid, as in other post-Eocene hystricognaths, is reduced in height, extending, in the temporal fossa, little if any above the level of the glenoid cavity (Figs. 12, 15A). It is separated from the frontal by a narrow strip of the orbitosphenoid, a significant difference from the African *Paraphiomys* (Lavocat, 1973: 31). Anteriorly, the alisphenoid forms the lateral wall of the foramen lacerum anterius. The dorsal border of the bone runs back in essentially a straight line, below the zygoma, to the front of the bulla. Ventrally, the alisphenoid forms the lateral wall of the pterygoid fossa, reaching the palatine just in front of the point where the pterygoid fossa begins (Fig. 15A). There is a broad shelf of the alisphenoid, behind the pterygoid fossa, separating the fossa from the large foramen lacerum medium (Fig. 15B). This seems to be homologous to the shelf in *Paraphiomys* (Lavocat, 1973: Pl. 2, Fig. 2) but differs in that, in the African form, it is at the level of the dorsal portion of the pterygoid fossa, whereas, in *Incamys* (Fig. 15B), it is ventral to the fossa. The fossa

and the foramen lacerum medium join dorsal to this shelf.

The pterygoid fossa is short, wide, very deep, and perforate (Fig. 15B). It is much wider than in *Neoreomys* or the living dasyproctids. We have been unable to determine what, if any, dorsal border there may have been to the pterygoid fossa, the alisphenoid wall being very thin, so that it is easy to cause damage inadvertently. Nor have we been able to detect any indication, within the dorsal fenestra, of a partition between the alisphenoid canal and the passage for *M. pterygoideus internus*. However, in view of the damage sustained by the specimen prior to burial and of the delicate nature of the bony separation in various hystricognaths, little significance can be attached to this. We believe that the openings in this region described here were all that were present in life; however, the thinness of the bone and the pre-fossilization damage that had occurred to the presphenoid, basisphenoid and basioccipital of PU no. 21945 (Fig. 15B) shows how much serious disintegration can occur, even in heavy bones on an otherwise well preserved skull. Lavocat's material of *Incamys* apparently did not preserve this area.

Along the medial wall of the fossa, there is a large opening, separating the internal pterygoid process from the presphenoid (Fig. 15B). This is the palatal opening of the choano-orbital fenestra discussed above. The function of this opening is not known to us. Comparable openings occur in some other hystricognaths, among them *Neoreomys* and the living dasyproctids. A thin bar of the presphenoid separates this fenestra from another one posteromedial to it, that lies mainly within the basisphenoid, although extending for a short distance into the presphenoid. We apply the noncommittal term sphenoidal fenestra to it, and confess total ignorance as regards its function (Fig. 15B; SF). We do not know of any other rodents in which this fenestra occurs.

The parietals have undergone crushing and buckling in most specimens, but are perfectly preserved in PU no. 21945 (Fig. 8A). They are, as shown by the dorsal contour of the occiput (Fig. 10B), much less arched transversely than those of *Neoreomys* and the living dasyproctids. In PU no. 21945 there seems to be a short section of suture still visible between the parietals (Fig. 8A); in other specimens, there is no trace of such a suture. The parietals resemble those of the Recent dasyproctids in general outline (Fig. 7), but the anterolateral corners extend forward (Fig. 8A), more as in *Neoreomys*. Faint, lyrate crests converging at the sagittal crest mark the medial limits of the weakly-developed temporal fossae. The sagittal crest is small and weak, as in *Myoprocta*. In contrast to *Platypittamys*, but in agreement with the great majority of caviomorphs (p. 488), there is no trace of a separate interparietal. Near the lateral margin of the parietal, directly above the porus acusticus externus, a fair-sized vascular foramen leads forward into the bone (Fig. 8A). The parietal extends, for the middle half of the width of the occiput, back almost to the top of the lambdoid crests. Laterally, however, the posterior margin of the parietal is bowed forward (perhaps indicating the lateral limits of the otherwise unidentifiable interparietal) by the lateral process of the occipital.

The squamosal is fundamentally similar to that of other members of the family. Posteriorly it is excluded from the occipital crest by the exoccipital. It is tightly appressed to the dorsal portion of the tympanic, but, in contrast to other dasyproctids, does not extend posteriorly beyond the porus. A small subsquamosal foramen is situated directly above the porus acusticus externus (Fig. 12); on the left side of PU no. 21945 this foramen is partially divided into anterior and pos-

terior portions. Anterodorsally, the squamosal extends to, and largely forms, the posterior postorbital process (Figs. 8, 12). The frontosquamosal suture bends backward, below the posterior postorbital process, and then runs almost vertically down behind the frontal to the level of the glenoid cavity. Below here, the frontosquamosal suture becomes highly crenulate, in contrast to the essentially smooth suture in modern dasyproctids and the slightly crenulate one in *Neoreomys*. Finally, this portion of the squamosal makes contact, ventrally, with the alisphenoid, slightly below the level of the glenoid (Fig. 15A). From here, the alisphenoid suture runs almost directly backward, below and medial to the glenoid cavity, until it reaches the front of the bulla. It is uncertain how far forward the squamosal extended on the zygoma; certainly no farther than the middle of the arch (Fig. 8).

The bulla is not preserved in the type; it is apparently partially preserved but still buried in the matrix in the type of *I. pretiosus* (Lavocat, 1976: 58), although we have been unable to recognize any trace of it in Lavocat's stereophotos (1976: Pl. 5, Figs. 6–7; Pl. 6, Figs. 4–5). In the skulls of PU nos. 21726 and 21945 (Figs. 10A, 12, 14), it is firmly attached and very large, about one quarter the length of the skull. It is roughly comparable in size to those of *Platypittamys*, *Chinchilla*, *Schistomys*, *Microcavia* and other small caviomorphs, and is relatively larger in all dimensions than those of other dasyproctids. Size apart, however, there is a similarity in shape and other features to the dasyproctid bulla. Widest and deepest anteriorly, the bulla of *Incamys* extends from a point in advance of the basioccipital-basisphenoid suture to the back of the condyle. The ventral surface is strongly arched, both anteroposteriorly and transversely. The anterior face is very gently convex. The anterior part of the medial surface is parallel to the long axis of the skull; the posterior part is inclined posterolaterally around the condyle (Fig. 15B). The basisphenoid and basioccipital press tightly against the anterior half of the bulla. In the posterior portion, where the bullae diverge, there is a narrow trench between the bulla and the basioccipital. The posterior portion of the trench is occupied by the foramen lacerum posterior (Fig. 15B). Partially separated from the anterior end of this is what seems to be another opening, leading forward. If this actually is a foramen, it may be a vestigial carotid canal, or it may have transmitted a vein. We incline to the latter alternative since some individuals of *Dasyprocta* have a similarly situated small opening, and Bugge (1974a: 54) found no trace of an internal carotid in that form. No other specimen of Deseadan caviomorph is sufficiently well preserved (and prepared) to demonstrate the presence or absence of this opening (see pp. 484–486 for a discussion of the carotid circulation in hystricognaths).

The porus acusticus externus is large and extends posterodorsally, imparting an oval outline to the opening (Fig. 13). Posteriorly, its rim forms a narrow ridge bounded behind by a deep and narrow groove. The tympanohyal articulation and the adjacent stylomastoid foramen are situated at the ventral extremity of the groove. The anteroventral lip of the porus acusticus is prominent and elevated on PU no. 21945, as in *Neoreomys*. There is a notch at the middle of the ventral wall of the porus, from which a deep, initially narrow, curving slit extends downward, then enlarging (Fig. 13), as in *Neoreomys* and young individuals of *Dasyprocta*, giving a figure eight shape to the opening. The anterior lip of the porus is somewhat thickened, but not so much so as in *Neoreomys*, and is perforated by a minute foramen. The porus is completely surrounded by the tympanic, as in rodents generally. Following Van Kampen (1905: Fig. 59), there has been some ten-

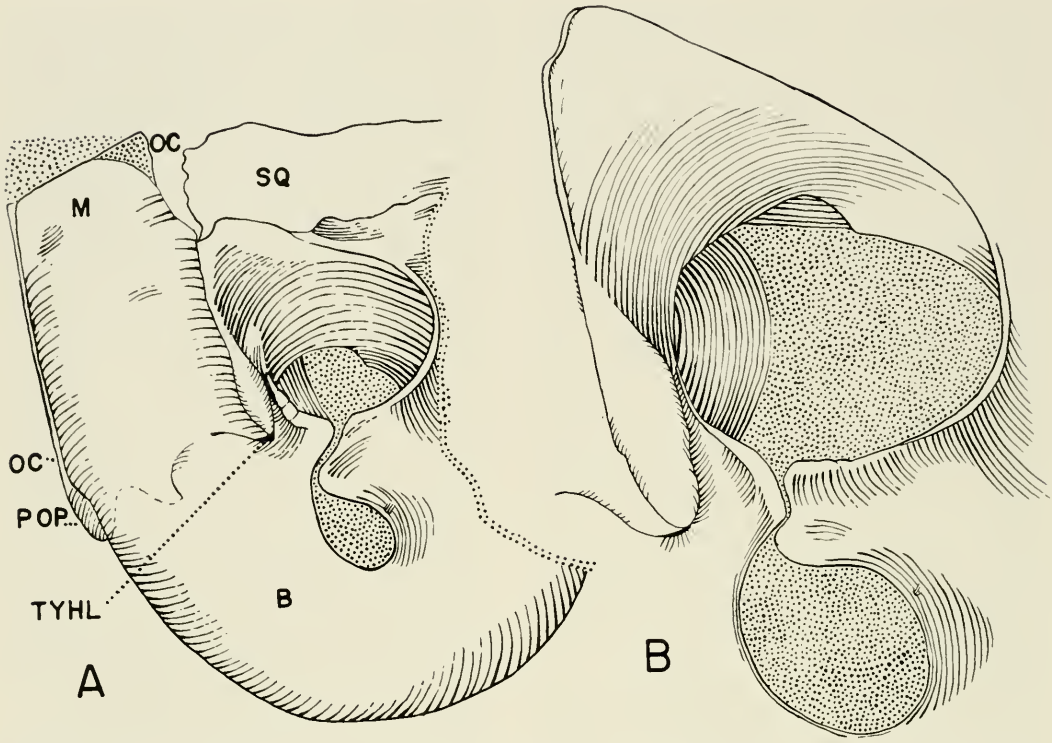

Figure 13. *Incamys bolivianus*, PU no. 21945, parts of right ear. A. Lateral view of bulla from somewhat behind and below, ×5. B. Lateral view of porus acusticus externus, ×10.

Abbreviations: B—bulla; M—mastoid process; OC—occipital; POP—paroccipital process; SQ—squamosal; TYHL—area of articulation of tympanohyal.

dency (e.g., Grassé and Dekeyser, 1955: 1334) to regard the portion of the bulla above the porus as being composed of the periotic. Evidence of its tympanic nature in rodents is, we believe, provided by certain paramyids, especially *Ischyrotomus oweni* (Wood, 1962a: 207), in which the bulla, found detached from the periotic, completely surrounds the opening of the porus. That part of the bulla dorsal to the porus is not so large as in other dasyproctids, especially posteriorly. A prominent groove runs backward from the anterior border nearly to the center of the anterior margin of the porus (Fig. 10); comparable, although shallower and more dorsally placed, grooves are present in *Neoreomys* and modern dasyproctids.

Posteriorly, the bulla narrows, as in other dasyproctids, and just reaches the short paroccipital process. Breakage in the right bulla of PU no. 21726 (Fig. 14A) reveals the lower part of the crista tympanica. The groove lateral to it is larger and deeper than in *Dasyprocta*, and is partially divided by at least three cross struts, features not present in the living forms. Within the matrix-filled tympanic cavity of PU no. 21726 are small pieces of bone; unfortunately, the extreme hardness of the rock has prevented further preparation, and it is impossible to determine whether these are exposed portions of the auditory ossicles or fragments of the bullar floor.

The mastoid process is large and in-

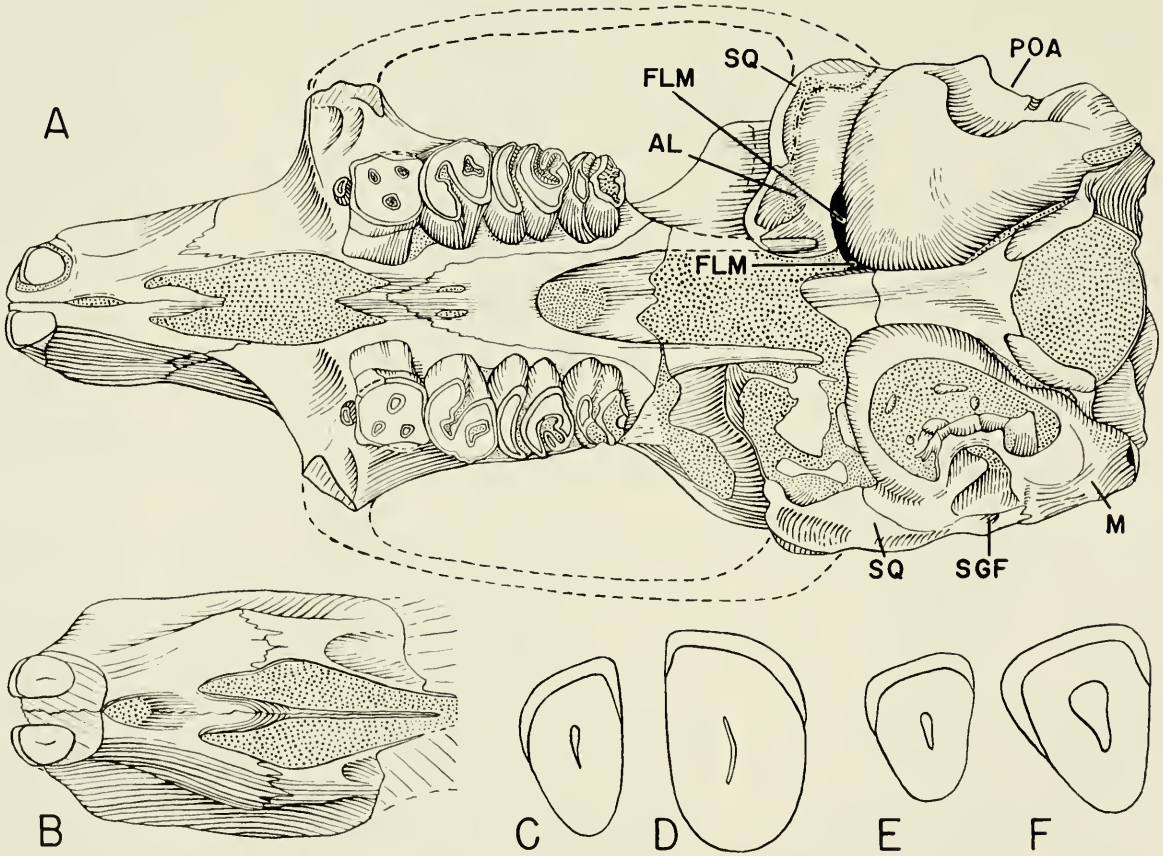

Figure 14. Skulls of *Incamys bolivianus*, ventral view, and incisors. A–B, ×3; C–F, ×10. Dotted areas are matrix. A. PU no. 21726, juvenile. B. PU no. 20944, partial skull. C. PU no. 21726, cross section of LI^1 from front. D. PU no. 20944, cross section of LI^1 from front. E. PU no. 21726, cross section of LI_1 from front. F. PU no. 21735, cross section of LI_1 below diastema.

Abbreviations: AL—alisphenoid; FLM—foramen lacerum medium; M—mastoid; POA—porus acusticus externus; SGF—supraglenoid foramen; SQ—squamosal.

flated, participating to a greater extent in the lateral surface of the skull than in other dasyproctids, and is visible in posterior view (Fig. 10B). Due to the inflation it merges smoothly with the posteroexternal surface of the bulla. A thin strip of the exoccipital, narrower than in other members of the family, separates it from the squamosal. Breakage on the left side of PU no. 21945 reveals that the inflated sinus of the mastoid was crossed by a number of septa. What may be the suture between the tympanic and the mastoid is shown in Fig. 13A, but we are not certain either that it is the suture or that we have located it correctly in its entirety.

The ventral part of the skull between the palate and the bullae is not preserved in the type (Lavocat, 1976: Pl. 3, Fig. 2), and in Lavocat's type of *I. pretiosus* only the endocranial surface has been prepared, which, as Lavocat stated (1976: 56), makes comparisons difficult. This area is badly broken in PU no. 21726, but part of it is very well preserved in PU no. 21945 (Fig. 15B). Even in this specimen, however, the ventral surfaces of the presphenoid, basisphenoid and basioccipital were damaged, before fossilization.

The presphenoid is a long, slender bone, its posterior end being just behind the anterior limit of the pterygoid fossa. Its posterior portion forms the median wall of the pterygoid fenestra. There is a lateral brace, near the posterior end of the bone, running posterolaterally to the alisphenoid and pterygoid, and forming the anterior border of the sphenoidal fenestra. The presphenoid is more slender, relatively, than in *Neoreomys*, and more comparable to that of *Myoprocta*.

Enough of the basisphenoid is preserved to reveal that there was an angle between it and the basioccipital on the ventral surface, comparable to that in other dasyproctids. Otherwise, it is badly damaged in all available specimens. Its anterior extremity surrounds most of the sphenoidal fenestra.

The basioccipital is widest at the condyles, narrows rapidly forward for half its length, and then maintains an even width for the remainder of its course. The ventral surface of the basioccipital in PU no. 21945 bears a strong median keel; its height is largely due to the crushing of the adjoining bone (Fig. 15B). The trench between the lateral margin of the basioccipital and the bulla has been described above. The foramen lacerum medium lies in front of the bulla at its junction with the basioccipital and basisphenoid.

The occiput is essentially vertical, as in *Neoreomys*. The supraoccipital is less arched than in that form or in the Recent dasyproctids, and extends over onto the dorsal surface only for a very short distance at the center (Figs. 7, 8A), in contrast to other dasyproctids but in agreement with *Platypittamys*; on the sides, however, it plays a larger part in the formation of the roof, agreeing in this with other dasyproctids and differing from *Platypittamys*. The lateral portion, separating the mastoid from the squamosal (Figs. 7, 8, 12; p. 487) starts out, at its mesial end, as a slender process between the central part of the parietal and the dorsal tip of the mastoid. It then widens considerably, separating the mastoid from the squamosal and lateral part of the parietal (Fig. 8A). At about mid-height of the squamosal, however, the process abruptly narrows (Figs. 10, 12, 13A) and extends as a very slender sliver of bone to just below the ventral limit of the squamosal, at the posterodorsal limit of the tympanic.

The suture between the exoccipital and the mastoid follows a ridge that runs laterally and a little dorsally from the upper part of the foramen magnum, as it does in other members of the family. Dorsal and ventral to this ridge are depressions for attachment of neck muscles (the depth of the dorsal one is exaggerated in PU no. 21726, Fig. 10B, due to breakage). There is an indication of a vertical crest running from the top of the foramen magnum to the occipital crest.

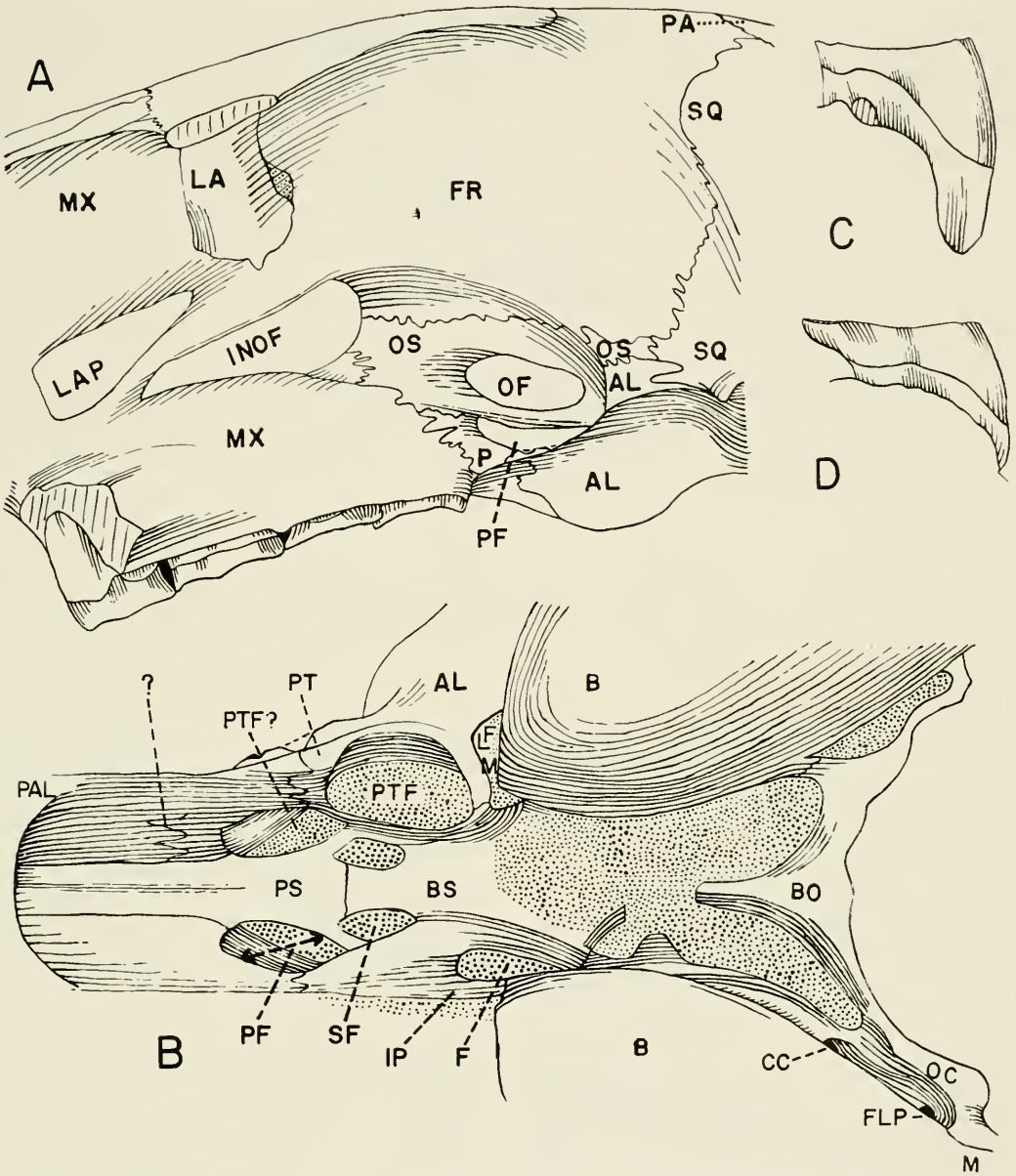

Figure 15. *Incamys bolivianus*, ×5. A–B. PU no. 21945, anterior end to the left. A. Oblique view of left orbit and temporal fossa. B. Ventral surface of basicranium. C–D. Posterior views of right upper molars, showing change in width of occlusal surface with wear. C. PU no. 20950, slightly worn M^1 or M^2. D. PU no. 20955, highly worn M^2.

Abbreviations: AL—alisphenoid; B—bulla; BO—basioccipital; BS—basisphenoid; CC—possible carotid canal; F—vacuity between internal pterygoid process and bulla; FLM—foramen lacerum medium; FLP—foramen lacerum posterior; FR—frontal; INOF—interorbital fenestra; IP—internal pterygoid process; LA—lacrimal; LAP—opening in wall of lacrimal canal; M—mastoid; MX—maxillary; OC—occipital; OF—optic foramen; OS—orbitosphenoid; P, PAL—palatine; PA—parietal; PF—choano-orbital orifice; PS—presphenoid; PT—pterygoid; PTF—pterygoid fossa; PTF?—possible extension of pterygoid fossa; SF—sphenoidal fenestra; SQ—squamosal; ?—probably a pseudosuture.

The paroccipital process is short, squat, and attached to the posterior surface of the mastoid and bulla, somewhat as in the octodontid *Sciamys* (Scott, 1905: Pl. 67, Fig. 9); in other dasyproctids it is longer and freely projecting.

The condyles are narrow, face ventrally as much as posteriorly—as in Recent dasyproctids—and lie closely alongside the bullae for much of their lengths. Inflation of the auditory region has brought much more of the lateral surface of the cranium into view from the occipital aspect than is the case in other members of the family. The foramen magnum is essentially circular and very large.

The mandibular fragments at our disposal (Figs. 12, 16) show that the horizontal ramus was approximately as deep and wide as that of *Cephalomys*. The posterior part of the dorsal border of the diastemal surface sloped gently downward and forward at almost the same angle as in that form and in *Neoreomys*, not so abruptly nor so deeply as in the living dasyproctids. The masseteric crest begins beneath the center of P_4 and agrees in size with those of other members of the family (Fig. 16A,B). The low coronoid (Fig. 16B) passes the alveolar level a little behind M_3, as in *Cephalomys*, and in contrast to the more forward position in later forms. The coronoid is clearly too large in Lavocat's reconstruction (1976: Fig. 3I). The condyle is an elongate oval, presenting dorsally, compressed laterally, and nearly on a level with the cheek teeth (Fig. 12); the postcondyloid process is moderately developed. The mental foramen is high and a little in front of P_4. It opens upward (Fig. 16B). A peculiar feature is the remarkable number of minute vascular foramina along the course of the incisors (Fig. 16D); none of Lavocat's figures show this area. Similar foramina, although not in such rich profusion, also occur in the living dasyproctids. As in the living forms, the posteroventral portion of the symphysis extends back beneath P_4. The genioglossal pit is very weakly developed.

Cement is lacking on all cheek teeth. The teeth are larger relative to skull size than in the living dasyproctids, being closer to *Neoreomys* in this respect. For terminology of the parts of the cheek teeth, see Figs. 1–2 (pp. 376–377). The upper teeth are inclined posteriorly, the lowers anteriorly. In both uppers and lowers the major lophs and lophids unite with wear into an S-shaped pattern, the S running from the lingual end of the anteroloph to the labial end of the posteroloph in the uppers and from the metaconid to the hypoconid in the lowers. This is especially evident after an intermediate amount of wear (Figs. 18A, 19G). The enamel over unworn crowns is thinner than that on the sides, as is shown by its thinness around the edges of lophs and lophids of slightly worn teeth.

The cheek teeth display unilateral hypsodonty, especially notable in the uppers which are hypsodont lingually and brachyodont labially (Fig. 17E). The mesodont lower teeth show much less disparity in height of crown, although the enamel descends lower on the labial and posterior faces (especially on the hypoconid) than on the lingual and anterior ones. This pattern for the initial stages in the development of hypsodonty is exceedingly common among the Rodentia, and cannot be taken to indicate any special relationships of *Incamys* with any other genus or group of genera.

The unilateral hypsodonty of the upper teeth results from the fact that there is no post-eruptional growth of the labial margin of the crown, whereas there is long continued growth of the lingual half of the tooth. As a result, eruption causes a tooth to rotate, in a transverse plane, about the buccal roots. The center of rotation is approximately at the point where the roots clear the alveoli. From this it ensues that there is extensive wear on the lingual half of the crown, and little wear on the extreme labial parts, which gradually extend farther and farther labially as rotation progresses. This is demonstrated by the posterior views of two up-

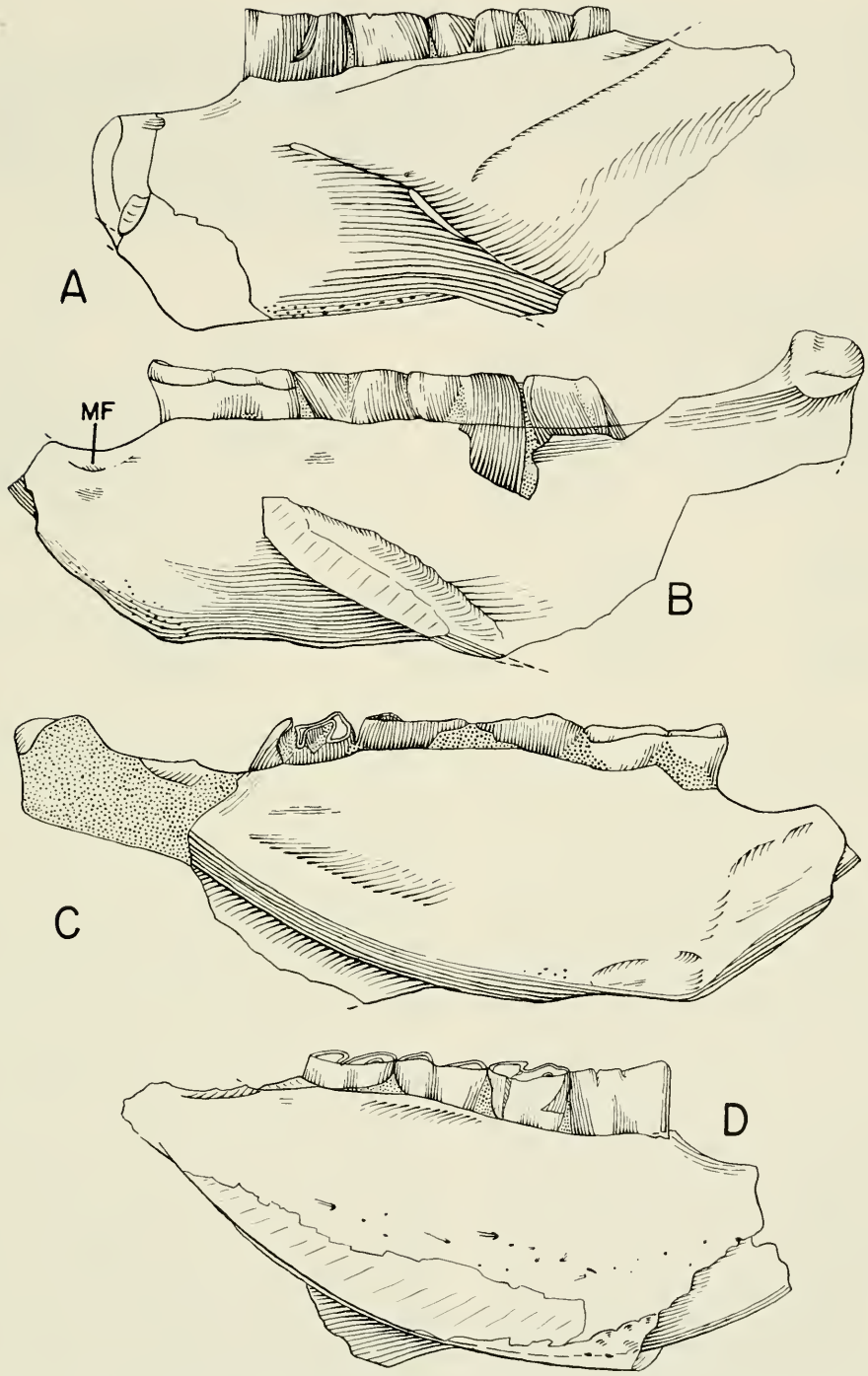

Figure 16. Lower jaws of *Incamys bolivianus*, ×4. Dotted areas are matrix. A. Lateral view of PU no. 20933, completed from PU nos. 20921, 20925, and 20941. B. Lateral view, PU no. 21726. C. Mesial view, PU no. 21726. D. Mesial view, PU no. 20933.

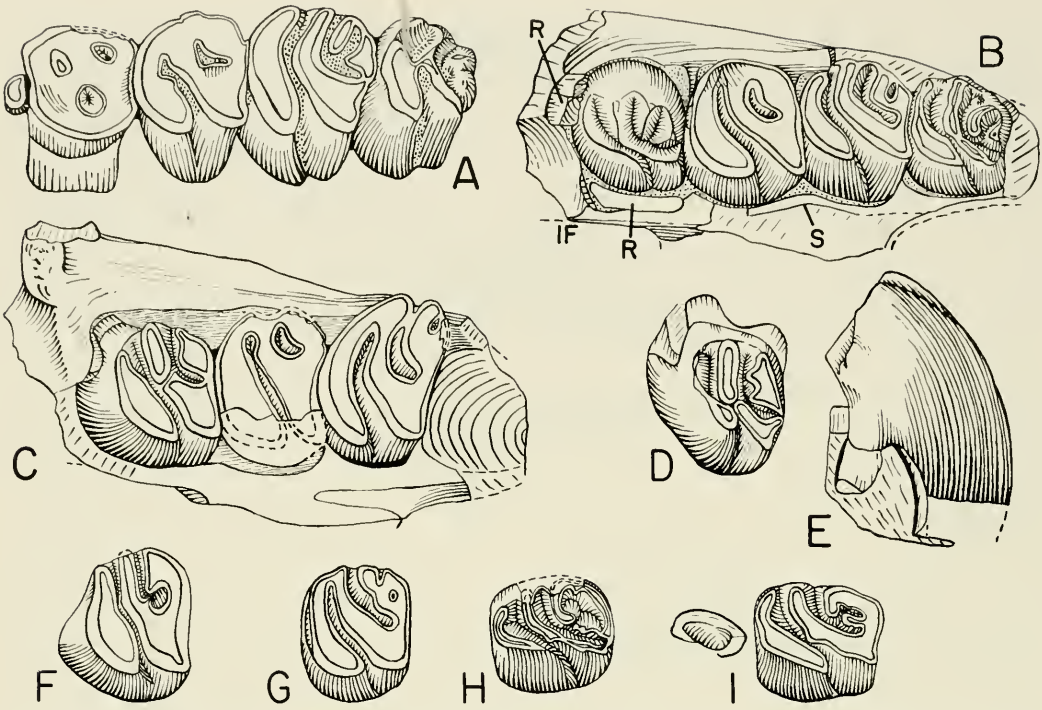

Figure 17. Left upper cheek teeth of *Incamys bolivianus*, anterior ends to the left, ×5. Dotted areas are matrix. A. PU no. 21726, dm^{3-4}, M^{1-3}. B. PU no. 21728, P^4–M^3. C. PU no. 20960, P^4–M^2. D–E. PU no. 20965, P^4. D. Occlusal view. E. Anterior view. F. PU no. 20963, P^4. G. PU no. 20968, $M^{1 \text{ or } 2}$. H. PU no. 20981, dm^4. I. PU no. 20980, dm^4 and root of dm^3.

Abbreviations: IF—incisive foramen; R—roots of dm^4; S—maxillary-palatine suture.

per molars. In the less worn tooth (Fig. 15C), the wear surface ends essentially ventrad of the labial margin of the buccal roots; in the worn tooth (Fig. 15D), the wear surface extends 1 mm or more beyond the labial margin of the roots. The situation just described is particularly characteristic of M^{1-2}. In both P^4 and M^3, the absence of adjacent teeth on one side has permitted the forward (or backward) growth of the hypsodont lingual portion, and the rotation of the tooth as eruption proceeds is not in a simple transverse plane. Therefore, these teeth do not increase so markedly in width with wear as do M^{1-2}, although an increase does occur (Table 3). The anteroposterior diameters of P^4–M^2 remain approximately constant as wear proceeds. That of M^3 increases in length with wear, but we have not computed σ and V for this tooth, as we did not have an adequate sample. Again, because of the size of the sample, we are not sure whether this tooth is or is not significantly smaller than the others (Table 3). P^4, however, does not differ greatly in size from the molars.

Lavocat (1976: 42) indicated that P^4 is smaller than M^{1-2}. This opinion is at least partly due to the fact that, of the three specimens he figured, two (the type, SAL 117, Lavocat, 1976: Pl. 4, Fig. 1 and SAL 118, Lavocat, 1976: Pl. 4, Fig. 2) have P^4 in process of eruption and the greatest diameters of these teeth are still intra-alveolar. The third specimen (SAL 163, Lavocat, 1976: Pl. 4, Fig. 4), which Lavocat referred to *I. pretiosus*, is an iso-

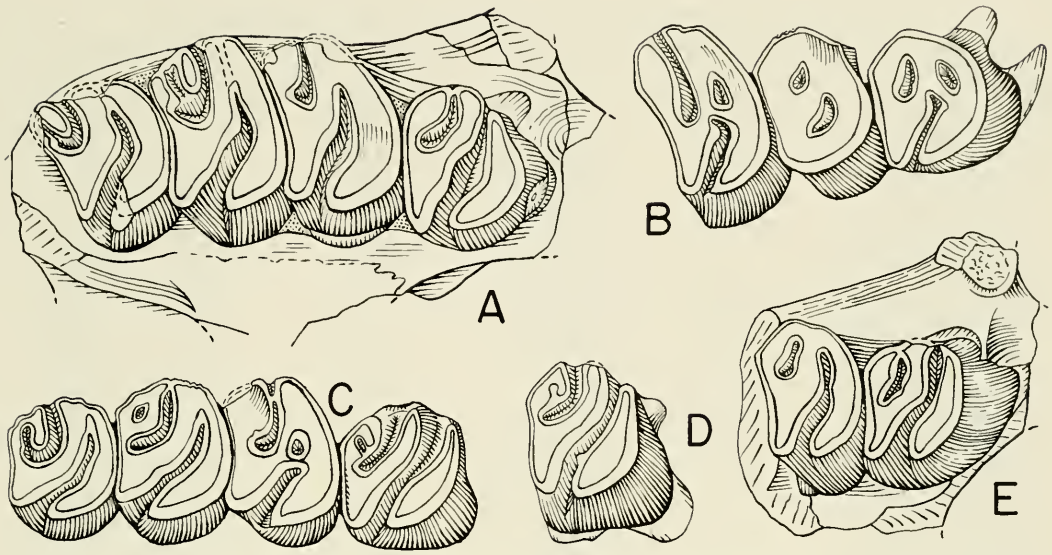

Figure 18. Right upper cheek teeth of *Incamys bolivianus*, anterior ends to the right, ×5. A. PU no. 20947, RP^4–M^3. Part of zygomatic root added from PU no. 20938; anterior part of maxillary-palatine suture from PU no. 20954. B. PU no. 20955, RP^4–M^2. C. PU no. 20943, RP^4–M^3. D. PU no. 20939, RP^4. E. PU no. 20956, RP^4–M^1.

lated P^4, and thus its size cannot be compared with that of M^1 or M^2.

In the lower teeth, P_4 is longer than the rest, and M_2 is the widest of the molars (Table 4). The most variable factor in the lower cheek teeth is the length of M_3. The length of the wear surface is to a great extent dependent on age, and is (otherwise) essentially meaningless. We have therefore taken the greatest extra-alveolar length of the crown as the anteroposterior diameter of the tooth. In cases where the entire alveolar border is preserved, we believe this measurement to be a homologous one. However, M_3 is implanted at an angle (Fig. 16B,C), so that the crown of the tooth extends a considerable distance behind the rear of the alveolus, within that cavity. A recheck of a number of specimens with unusually large anteroposterior diameters for M_3 showed that in most cases the unusually long measurements resulted from the fact that the posterior margins of the alveolus were damaged or destroyed.

Because of the element of uncertainty as to the length of M_3 and the variation of transverse diameters of M^{1-2} with age, we have prepared Tables 3–4 both to include all specimens as originally measured and to exclude the anteroposterior diameters of M_3 where the location of the posterior margin of the alveolus is uncertain and the transverse diameters of all specimens of M^{1-2} where the buccal margin of the crown extends 1 mm or more beyond the labial margin of the roots (Fig. 15D).

Lavocat (1976: 42–43) discussed the homologies of the various parts of the upper cheek teeth of *Incamys*. We are in agreement with him that the anterior crest is an anteroloph uniting lingually with the protocone, and that the second crest is the protoloph uniting lingually with the hypocone. On the labial sides of the crowns of unworn teeth there are two large, subequal cusps, continued lingually by ridges reaching about halfway across the teeth (Fig. 17A, M^{2-3}; 17B, P^4,

TABLE 3. MEASUREMENTS, IN MM, OF UPPER TEETH OF *Incamys bolivianus*.

	N	OR	$\bar{X}$	σ	V
P^4–M^3 or dm^3–M^3	7	11.2–14.0	12.70		
dm^3 anteroposterior	2	.61–.68	.65		
transverse	2	1.08–1.27	1.18		
dm^4 anteroposterior	5	2.83–3.47	3.14		
width protoloph	4	2.81–3.68	3.30		
width metaloph	2	2.95–3.47	3.21		
P^4 anteroposterior	21	3.04–4.11	3.59	±.29	8.05
width protoloph	21	3.28–4.50	3.77	±.27	7.16
width metaloph	20	3.25–4.36	3.85	±.36	9.35
M^1 anteroposterior	22	2.61–3.30	2.91	±.17	5.84
width protoloph*	16	3.40–5.8	4.15	±.56	13.49
width protoloph#	13	3.40–4.60	3.98	±.37	9.30
width metaloph*	13	3.32–5.8	4.03	±.73	18.11
width metaloph#	10	3.32–4.24	3.69	±.26	7.05
M^2 anteroposterior	14	2.68–3.48	3.00	±.22	7.33
width protoloph*	15	3.40–5.68	4.13	±.76	18.40
width protoloph#	12	3.40–4.29	3.80	±.31	8.16
width metaloph*	13	3.44–5.6	4.14	±.71	17.15
width metaloph#	10	3.44–4.51	3.80	±.32	8.42
M^3 anteroposterior	9	2.43–3.39	2.87		
width protoloph	8	2.84–4.54	3.61		
width metaloph	6	2.81–3.48	3.12		
I^1 anteroposterior	5	2.35–3.13	2.76		
transverse	6	1.40–2.13	1.72		
ratio	5	.60–.70	.64		

* Including all specimens.

Excluding PU nos. 20929, 20947, and 20955. The rationale for making computations omitting these specimens is discussed in the text.

M^{2-3}; Lavocat, 1976: Pl. 4, Fig. 1, P^4). At the rear of the teeth is a crest that we and Lavocat agree is the posteroloph.

The crux of our differences lies in the nature of the two labial cusps. We believe them to be the paracone and metacone (Fig. 1A–C; PA, ME), as they are subequal and occupy the normal mammalian positions for such cusps. Lavocat accepts the anterior as the paracone, but interprets the second as the labial end of the mesoloph, more specifically (1976: 45) as a mesostyle, which would therefore (although he does not say so) mimic the normal metacone. Lavocat (1976: 42) stated that the structures of this area in the thryonomyoids "sont morphologiquement absolument comparables." We cannot understand this statement, since the upper teeth of the most primitive known thryonomyoid, *Phiomys andrewsi* of the early Oligocene (Fig. 30C), have a paracone and metacone (recognized as such by him) fundamentally like what we consider to be the paracone and metacone in *Incamys*, but separated by one or more intermediate crests (two in Fig. 30C), at least one of which must be the mesoloph. A very similar pattern is present in the more advanced *Metaphiomys schaubi* (Fig. 30D), also from the early Oligocene. In *Incamys*, there certainly is no trace of a crest that could be a mesoloph between what we believe to be the paracone and metacone.

Lavocat pointed out that some thryonomyoids such as *Gaudeamus*, with a reduced number of crests, are found in association with the more primitive five-crested ones. He is entirely correct in this, and *Gaudeamus* is also clearly specialized in being somewhat higher

TABLE 4. MEASUREMENTS, IN MM, OF LOWER TEETH OF *Incamys bolivianus*.

	N	OR	$\bar{X}$	σ	V
P_4–M_3, alveolar	4	12.5–14.0	13.4		
dm_4–M_3, alveolar	2	15.5–15.9	15.7		
dm_4 anteroposterior	3	ca. 3.8–5.21	4.45		
width metalophid	3	1.94–2.43	2.10		
width hypolophid	4	2.65–2.96	2.78		
P_4 anteroposterior	22	2.97–4.24	3.67	±.32	8.72
width metalophid	20	2.14–3.09	2.64	±.24	9.09
width hypolophid	21	3.03–3.61	3.28	±.20	6.09
M_1 anteroposterior	27	2.67–3.57	3.12	±.24	7.70
width metalophid	18	2.86–3.87	3.38	±.26	7.69
width hypolophid	22	2.93–3.85	3.44	±.23	6.69
M_2 anteroposterior	25	2.65–3.51	3.19	±.25	7.84
width metalophid	19	2.78–4.15	3.55	±.35	9.86
width hypolophid	23	2.99–4.05	3.58	±.28	7.82
M_3 anteroposterior	13	2.95–3.78	3.26	±.28	8.59
revised ant. post.*	11	2.95–3.50	3.17	±.20	6.31
width metalophid	12	2.85–3.68	3.29	±.24	7.30
width hypolophid	14	2.64–3.50	2.97	±.22	7.41
I_1 anteroposterior	29	1.85–2.63	2.20	±.22	10.00
transverse	31	1.38–2.01	1.61	±.15	9.32
ratio	29	.61–.84	.73	±.05	6.85

* The anteroposterior measurements of two specimens (PU nos. 21952 and 22335) were omitted for this calculation, as the alveolus was so damaged that anteroposterior measurements were not accurate.

crowned and notably more lophate than the five-crested genera. Lavocat then argued (1976: 43) that we should agree that four-crested genera in the Deseadan should likewise be recognized as derived from something like the contemporaneous five-crested forms. But, in the Deseadan, the majority of the low crowned and clearly cuspidate genera have four-crested upper teeth (*Platypittamys*, *Deseadomys* and *Sallamys*; *Protosteiromys* is the only exception), whereas the higher crowned and lophate genera are frequently five-crested (*Cephalomys*, *Branisamys* and the unnamed genus discussed on p. 430; we do not know how many crests there were in the upper teeth of *Scotamys*). *Incamys*, with an intermediate stage in the development of hypsodonty, has upper teeth that do not show a fifth crest. As a result, Lavocat is forced to argue that all of the primitive looking Deseadan rodents are specialized, a conclusion that seems to us to make sense only if one adopts the preconceived idea that five-crested teeth are necessarily primitive—a point to which we shall return below (pp. 493–495).

According to Lavocat (1976: 42), careful observation of upper teeth of *Incamys* revealed a tubercle, distinct from the posteroloph, at the labial extremity of the latter, which he considered to be the metacone. Unfortunately, he gave no indication as to which specimens showed such a structure, and we could find no indication of its presence, either on his stereophoto (1976: Pl. 4, Fig. 1) or on any of the Princeton specimens (e.g., Fig. 18B)—or, indeed, of anything other than normal minor irregularities of the posteroloph. Lavocat also reported what he considered to be a variable and reduced metaloph lying on the anterior flank of the posteroloph. His figure of P^4 of the type (1976: Pl. 4, Fig. 1) shows what may be such a structure, well down in the deep valley; we cannot determine whether or not a similar structure is present on M^2 of the same figure. This type

of structure, deep within a valley of a tooth that is evolving toward hypsodonty, is secondary, a neomorph, as indicated clearly in Recent dasyproctids (Fig. 20J), and not a degenerating metaloph. SAL 118, which Lavocat referred to *I. bolivianus*, does have a projection in this position on all teeth preserved, but this specimen represents an undescribed dasyproctid genus (p. 430).

The upper premolar is submolariform. It is more advanced in structure and larger relative to the molars than those of contemporary octodontoids, smaller relatively but somewhat more advanced structurally than those of *Cephalomys* and *Scotamys*, less advanced than that of *Branisamys*. In unworn or little worn specimens (Fig. 18B–D), the anteroloph slopes upward and a little forward from the protocone and then curves posteriorly to join the paracone near its base. Lavocat (1976: 45) noticed this condition in the type, but concluded that the difference from the situation in the molars is due to reduction, whereas we believe that the premolars of *Incamys* were in the process of molarization, and that the anteroloph was developing.

A cuspule may or may not be present at the labial end of the anteroloph; in one specimen, PU no. 20929, there is a cuspule at the base of the paraflexal notch, and in another, PU no. 20947 (Fig. 18A), at the base of the center of the anteroloph. The protocone is almost wholly subordinated in the crest. The protoloph is robust, thick, and abuts against the lingual portion of the anteroloph. The hypocone is sharply angulate lingually and slightly concave posteriorly toward the tip. It sends a blunt projection antero-externally, the mure (interpreted by Lavocat, 1976: 45, as the mesoloph), that comes into contact with both protocone and protoloph, and a smaller, pointed one that touches the posteroloph. The latter crest is expanded anteriorly at its labial end as a smoothly curving bulge in a few specimens (e.g., PU nos. 20960, 20943; Figs. 17C, 18C). A metaloph is in the process of developing, however, and this region of the tooth is in consequence extremely variable. Metaloph differentiation ranges from nil, as in the teeth just mentioned, to well developed (PU no. 21728, Fig. 17B), with all intermediate stages represented. In some specimens, e.g., PU no. 20965 (Fig. 17D), two small, angular projections extend forward from the anteroloph. The metaloph of P^4, when present, fails to reach the mure, as is also the case in the molars. The paraflexus is wide, and both it and the mesoflexus are much deeper in the middle of the tooth than are the notches that separate the paracone from the anteroloph and the metacone from the posteroloph. These notches are variable in depth; the former may or may not be deeper than the latter. The hypoflexus is well developed, extending up the crown for over half its height. As wear progresses, the spurs from the hypocone soon unite with the protoloph and posteroloph, but the separation of the anteroloph from the protoloph, on the contrary, increases. A cleft opens between these lophs, and the hypoflexus becomes confluent with the paraflexus, remaining so until about half of the tooth has been worn away. Anteroloph and protoloph then become joined labially (Fig. 18A,E), the hypoflexus remaining open until a very advanced stage of wear. Before lingual closure takes place, a parafossette is isolated when wear reaches a small isthmus that connects the anteroloph to the protoloph deep within the combined para- and hypoflexus. The mesoflexus is converted to an anteriorly curving fossette either slightly before or at about the same stage as the labial union of antero- and posteroloph. The grinding surface as a whole increases greatly in width as wear progresses, due to the marked unilateral hypsodonty (see above, p. 416), which is comparable to that occurring in *Cephalomys*. As in that genus, V for these values is high (Table 3).

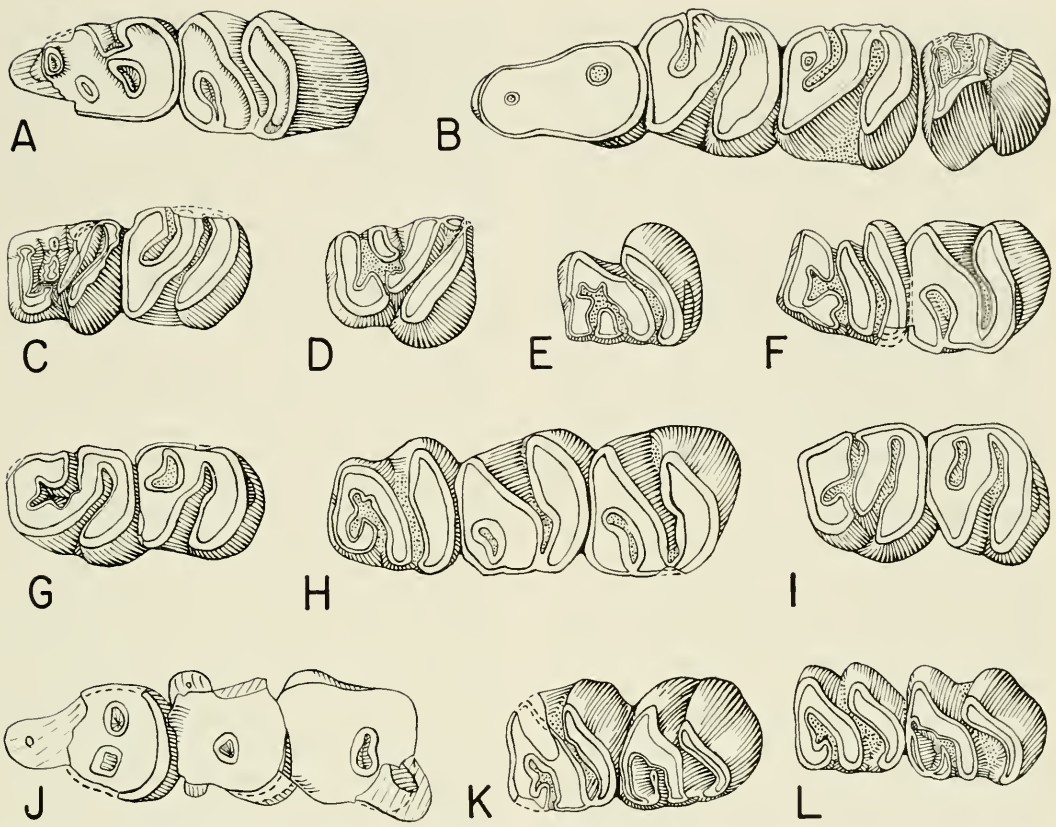

Figure 19. Lower cheek teeth of *Incamys bolivianus*, ×5. Dotted areas are matrix. A. PU no. 20921, Rdm_4–M_1. B. PU no. 21726, Ldm_4–M_3, partly restored from right side. C. PU no. 20975, LP_4–M_1. D. PU no. 20918, LP_4. E. PU no. 20930, RP_4. F. PU no. 20919, RP_4–M_1. G. PU no. 20935, LP_4–M_2. H. PU no. 20937, RP_4–M_2. I. PU no. 20948, RP_4–M_1. J. PU no. 21735, LP_4–M_2. K. PU no. 20936, RM_{1-2}. L. PU no. 20916, RM_{2-3}.

Unworn or little worn upper molars (Fig. 17A,B; Hoffstetter and Lavocat, 1970: Fig.; Lavocat, 1976: Pl. 4, Fig. 1) are approximately as long as wide at the occlusal surface and are tetralophate, sometimes with a minute projection from the anterior slope of the posteroloph of M^{1-2}. As in P^4, the anteroloph is usually separated from the combined protoloph and mure by a deep hypoflexus, but, in contrast to P^4, the labial notch, the paraflexus, between the two crests is very shallow (Figs. 17B, M^1; 17G, M^1 or M^2; 18A,C, M^3). The hypoflexus becomes progressively more extensive, vertically, in the posterior part of the molar series. On M^1 it extends up for approximately half the height of the crown, on M^2 rather more, and on M^3 it comes close to the base of the enamel (PU no. 20947, Fig. 18A, is exceptional in having an extensive hypoflexus on M^1). The protoloph sweeps lingually and posteriorly to the hypocone, which is also connected from the beginning of wear with the posteroloph. On the anterior face of the latter crest, a small projecting crestlet is present on M^{1-2}. The metaloph does not meet the protoloph. The mesoflexus has the deepest labial notch, and the metaflexal

notch is almost as shallow as the paraflexal one. The metaflexus is short. Due to the shortness of the metaloph, the mesoflexus extends postero-internally to the posteroloph, joining the metaflexus. Moderate wear soon obliterates much of the detail. Paraflexus, metaflexus and crestlet disappear, the metaloph joins the posteroloph, transitorily isolating a shallow metafossette in all except PU no. 20947 (Fig. 18A), and the crown surface progressively widens. With further wear, the mesoflexus converts to an anteriorly curving fossette and a parafossette is isolated when the deeply situated isthmus connecting anteroloph and protoloph is reached, as in P^4 (Fig. 18). In the terminal stages, the hypoflexus converts to a fossette, the parafossette disappears, the mesofossette becomes irregularly pear-shaped in outline, and the convexity of the anterior faces and the concavity of the posterior ones become decidedly pronounced.

The upper cheek teeth resemble in many ways those of *Branisamys* (Figs. 23, 24). They differ in being higher crowned and shorter relative to width, in lacking neolophs, and in having shorter metalophs that fail to reach the protolophs. A basic resemblance also exists between the upper molars of *Incamys* and *Neoreomys* (Wood and Patterson, 1959: Fig. 17A), and between the upper cheek teeth of *Incamys* and *Scotamys* (Wood and Patterson, 1959: Fig. 8). Resemblances to living dasyproctids are discussed below (pp. 427–429).

The lower cheek teeth are four-crested (Fig. 19B, M_3; C, P_4; D, P_4; E, P_4; F, P_4; H, P_4; K, M_{1-2}; L, M_{2-3}). The anterior part of P_4 is longer than the posterior, as Lavocat noted (1976: 46), and the anterior part of the molars has a greater area than does the posterior. On many molars, there is a crest extending buccad from the metaconid that ends freely (Fig. 19B, M_3; K, M_{1-2}; L, M_{2-3}; Lavocat, 1976: Pl. 3, Fig. 3, M_2; Fig. 4, M_{1-2}; Fig. 6, M_1; Fig. 7, M_{1-3}). There seems to be no reason to doubt that this is the posterior arm of the metaconid that does not reach the protoconid to form a metalophid (or metalophulid II; Wood and Wilson, 1936); Lavocat (1976: 47) considers this crest to be a mesolophid, a crest with which it has not the slightest resemblance either in position, shape, or relationships.

P_4 is tetralophate, longer than the molars, and broader across the talonid than the trigonid. The anterolophid is transverse. The metalophid is variable as to size and degree of development (Fig. 19). In little worn teeth it is an independent, more or less transverse crest, but it soon becomes connected by wear to the posterior face of the metaconid. The posterior arm of the protoconid is connected, in some specimens early, in others rather late, to the hypolophid (in which the ectolophid is incorporated). The latter is joined, after slight wear, to the posterolophid, which curves antero-externally to the sharply angulate hypoconid. On eruption, the posterolophid touches the hypolophid (Fig. 19C), but the two crests separate as wear proceeds, just as do the anteroloph and protoloph of P^4. There is a small spur from the protoconid extending toward, but not fusing with, the metalophid, and there may or may not be one extending posteriorly from the center of the anterolophid. The trigonid may be somewhat twisted labially with respect to the long axis of the talonid, as in PU no. 20919 (Fig. 19F). The hypoflexid is deep and wide, extending downward nearly to the base of the enamel on the labial side. The metaflexid is confluent with it, and the metaflexidal notch is very shallow. Development of the mesoflexid is variable. In little worn specimens it crosses the tooth. Thereafter it may be closed off lingually at a rather early stage of wear or may persist until a considerably later one (cf. PU nos. 20937 and 20948, Fig. 19H–I). The anteroflexid is confluent with the deeper and larger mesoflexid, due to the separation of metalophid and protoconid. In little worn specimens there is a shal-

low notch between protoconid and anterolophid (cf. *Neoreomys*, Scott, 1905: Pl. 65, Fig. 9, and *Scotamys*, Wood and Patterson, 1959: Fig. 9A). With deep wear the combined anteroflexid-mesoflexid would convert to a fossettid. The hypoflexid ultimately converts to two fossettids (Fig. 19J).

The lower molars are basically tetralophate, although the metalophid is incomplete (Fig. 19). Trigonid and talonid are approximately equal in width in M_{1-2}; in M_3 the talonid is narrower (Table 4). The anterolophid is again transverse and is joined to the obliquely-running hypolophid in the unworn teeth; as in P_4, a small spur may or may not project posteriorly from it toward the posterolophid (Fig. 19B; M_3). The short transverse metalophid was apparently joined to the metaconid in the unworn state (Fig. 19B,K; Lavocat, 1976: Pl. 3, Fig. 4, Fig. 7 M_3). The large, oblique posterolophid approaches the hypolophid labially on unworn teeth (Fig. 19B), but the cleft between them widens with wear. Lingually, the two crests are separated by the shallow metaflexidal notch. The combined hypoflexid and metaflexid is large, deep, and extends nearly to the base of the enamel on the labial sides of M_{2-3}; on M_1 its extension is variable. The combined meso- and anteroflexid is comparatively shallow and of variable shape. There is a minute, ephemeral fossettid at its anterolabial extremity in one specimen (PU no. 20916, Fig. 19L). The inclination of the protoconid varies from lateral to somewhat posterolateral. After moderate wear the meso- and metaflexidal notches disappear, the lingual wall of the tooth becomes continuous, the hypoflexid widens, the metalophid loses all individuality, and the combined antero- and mesofossettid becomes slit-like; in one specimen (PU no. 21726) a small anterofossettid is briefly isolated. With deep wear the posterolophid and the hypolophid become joined by an isthmus, isolating a rounded metafossettid, the mesofossettid shortens, and the hypoflexid closes. The final stage revealed by our material is a rounded hypofossettid in an otherwise featureless crown surface, with the enamel eliminated from considerable parts of the periphery of the crown (Fig. 19J).

As in the case of the upper cheek teeth, the lowers exhibit a close resemblance to those of *Branisamys*, differing chiefly in their greater height of crown and shorter, freely projecting metalophids. Again, there is a basic resemblance to *Neoreomys* in molar structure, and a less precise one to *Cephalomys*. Comparisons with living dasyproctids are made below (pp. 427–429).

As in *Branisamys*, dm^3 was single rooted. It is a small, rather peg-like tooth, wider than long, convex anteriorly and concave posteriorly (Fig. 17A). Dm^4 (Figs. 14A; 17A,H,I) is much shorter crowned than the molars, although the degree of unilateral hypsodonty is essentially the same. In the unworn state the crown is longer relative to width than in the molars, but as wear progresses the length decreases and the width increases until, shortly before being shed, the tooth becomes square. The tooth is tetralophate, a much longer spur extending forward from the posteroloph than occurs in the molars. The anteroloph and protoloph form stout crests, the former extending posteriorly for a little over half the length of the tooth, the latter merging with the sharply angular hypocone. The metaloph fails to meet the protoloph, as in the permanent upper cheek teeth. The posteroloph continues around the labial face, where it joins the metaloph. From this portion of the crest a small spur (barely visible in PU no. 20980, Fig. 17I) projects lingually. The hypoflexus persists to within a short distance of the base of the enamel. In apparent contrast to the molars, it does not appear to be confluent with the paraflexus, the protocone and anteroloph in PU nos. 20980 and 20981 (Fig. 17H,I) giving every appearance of

having joined at a very early stage of wear. The paraflexus is very large, deep and expanded anteroposteriorly. The mesoflexus, due to the incomplete metaloph, sweeps posteriorly to join the large, shallow and partially divided metafossette. Deep wear is shown by PU no. 21726 (Fig. 17A). Three fossettes, two labial and one lingual, are all that remains of the crown pattern; these are, respectively, the para-, meta-, and hypofossette.

The tooth provisionally identified by Scott (1905: 390; Pl. 65, Fig. 3) as dm^4 of *Neoreomys* is similar to that of *Incamys*, differing in the union of metaloph and protoloph, and in the presence of a small neoloph. We believe Scott's provisional identification to have been correct.

Four specimens of dm_4, all deeply worn, are available to us. They reveal that the tooth was long and narrowed anteriorly. Two preserve the last remnant of the hypoflexid and three fossettids (Fig. 19A). The posterior of these is clearly the metafossettid, and the intermediate one is presumably the mesofossettid. The anterior may be a feature of the deciduous dentition, analogous to the posterior fossettid of the trigonid of *Myoprocta*. A less worn tooth (Lavocat, 1976: Pl. 3, Fig. 3) shows four fossettids. Lavocat considered it to be essentially identical to one type of dm_4 in the early Oligocene thryonomyoid *Phiomys andrewsi* (Wood, 1968: Fig. 1G). Lavocat's figures (1976: Fig. 21,K) show that both are elongate teeth, but to us his figures strongly suggest that a more meaningful comparison could be made with dm_4 of *Cephalomys* (Fig. 26B). We find Lavocat's description somewhat difficult to interpret, especially since the pattern shown in his drawing (1976: Fig. 21) seems to differ in many respects from that shown by his stereophoto (1976: Pl. 3, Fig. 3). We continue to believe that interpretation of uncertain tooth structures in Deseadan rodents should be based on comparisons with other South American rodents and not with African ones.

The incisors are slender, rather small, and D-shaped in outline. The anterior face is more rounded in juveniles than in adults (Fig. 14C–F), particularly in the case of the lower incisors. The thick enamel extends much farther onto the lateral than onto the mesial face. The uppers extend back into the maxilla to a point slightly in front of and well above P^4. The lowers pass beneath the cheek teeth at the level of M_2 and terminate posterior and lateral to M_3. In all these respects they closely resemble the incisors of *Myoprocta acouchy*. The incisors are relatively much more slender than in *Branisamys*. The disparity in size between the incisors of PU no. 21726 (Fig. 14C,E) and those of PU nos. 20944 (Fig. 14D) and 21735 (Fig. 14F) is due to age. The first is a juvenile, the other two adults, and rodent incisors increase in diameter as growth proceeds.

Relationships. Hoffstetter and Lavocat (1970: 173) called attention to a resemblance between the lower molars of *Incamys* and those of the Fayum thryonomyoid *Gaudeamus*. Lavocat (1976) placed *Incamys* in the Dasyproctidae, but gave no reasons, and his comparisons were largely with non-dasyproctid genera, especially African thryonomyoids. The resemblance of *Incamys* to some specimens of *Gaudeamus* (although by no means to all—cf. Wood, 1968: Figs. 14, 15) exists, but this is more than offset by major differences in the premolars and in the upper molars. Affinities do not, we believe, lie in this quarter. As pointed out above, there is a very close resemblance between *Incamys* and *Branisamys* in cheek tooth structure, but differences in the skull rather definitely point to a broad rather than a narrow relationship between the two.

The known form to which *Incamys* is most closely related is beyond doubt the Santacruzian *Scleromys* (Scott, 1905: 401–403, Pl. 65, Figs. 13–15), as Hoffstetter (1968: 1096) originally believed. The two resemble each other closely insofar

as they can be compared. In both, the incisors are relatively small, the patterns of upper and lower cheek teeth are very close at comparable stages of wear, and the tooth rows are nearly parallel. The snouts are similar as regards parallel-sidedness, position of the premaxillary-maxillary suture in relation to the very large incisive foramina, and the size and relations of the fossae for *M. buccinator*. *Scleromys* differs from *Incamys* in having cheek teeth that are somewhat longer anteroposteriorly, a snout that is longer relative to the length of the cheek-tooth row, and a relatively wider palate that lacks a groove running back from the incisive foramina, and is somewhat less excavated posteriorly by the choanae. These distinctions are such as might be expected between earlier and later closely related forms, and do not, in themselves, rule out the possibility of ancestor-descendant relationships.

As we have previously intimated (1959: 328), we do not believe that the Colombian Friasian species, *schurmanni* and *colombianus*, placed in *Scleromys* by Fields (1957), really belong to it. As he pointed out, they resemble dinomyids in various features, and we believe they should be placed in that family. *Scleromys* was a dasyproctid. The Colombian species may for the present be referred, with a large query, to the Patagonian Friasian dinomyid *Simplimus* Ameghino. The type species, *S. indivisus*, is larger than the Colombian ones, but poorly known. Nevertheless, the various cheek teeth figured by Kraglievich (1930c: Figs. 2, 4) agree in structure with stages of wear in *colombianus* revealed by Fields' sections (cf. Kraglievich, Fig. 2 with Fields, Fig. 14, P^4 at stage 2; his Fig. 4, center, with Fields, Fig. 14, P^4 at stage 5; and his Fig. 4, left, with Fields, Fig. 14, P_4 at stage 1). The femoral and tibial fragments, the calcaneum, and the astragalus referred by Kraglievich (1930c: Pl. 1) to *Simplimus indivisus* may represent another dinomyid. They are disproportionately large relative to cheek-tooth size, much more so than in *S. colombianus* and *Drytomomys*.

Stirton's record (1953: 61) of *Scleromys*? from the Coyaima faunule of Colombia is very dubious. Neither the generic identification nor the Colhuehuapian age assigned to the deposit can be regarded as established.

Most of the extinct dasyproctids so far discovered were neither involved in nor near to the ancestry of the surviving forms. *Cephalomys*, *Litodontomys* and *Olenopsis* (if they are correctly placed here) would appear to represent side branches (Wood and Patterson, 1959: Fig. 12). *Neoreomys*, the best known of the extinct dasyproctids, is clearly a member of a lineage pursuing an evolutionary path that was not heading in the direction of *Dasyprocta* and *Myoprocta*. *Incamys* and *Scleromys*, however, appear to us to be close to the ancestry of the living genera.

This is particularly evident in the cheek teeth (Fig. 20). Worn uppers and lowers of the living forms display a short hypoflexus and hypoflexid and an almost bewildering array of small fossettes and fossettids (Fig. 20E,F), patterns which at first glance seem almost to defy interpretation. Examination of freshly erupted or unerupted teeth, however, reveals simpler patterns (Fig. 20A–D,G–I) that basically resemble those of *Incamys* (Fig. 17B–D), and which clearly show the S-arrangement of the lophs and lophids that occurs in that form and in *Scleromys* (see Hagmann, 1907: Figs. 25–26 for the same pattern in *Dasyprocta*). The profusion of fossettes and fossettids that characterizes worn *Dasyprocta* and *Myoprocta* cheek teeth comes about not so much from structures at the apex of the tooth, as from variable projections and pillars that arise at various depths within the tooth, from the surrounding enamel walls of the lophs and lophids and also, independently it would seem, from the bottoms of valleys (Fig. 20J and Hag-

mann, 1907: Pl. 26, Fig. 9). A neoloph and a neolophid are present in the cheek teeth of the living species, the former arising from projections extending anteriorly from the anterior wall of the posteroloph and lingually from its antero-labial extremity; in *Incamys* the first of these is sporadically present. (Here is clear evidence, we believe, of a neoloph arising within one lineage of a family after the same crest had come into existence in two other lineages, those of *Cephalomys* and of *Neoreomys*.) The neolophid appears to arise from the base of the tooth and to participate in the grinding surface only after considerable wear (Hagmann, 1907: Pl. 26, Fig. 9; redrawn here as Fig. 20J). Upper cheek teeth of *Dasyprocta* and *Myoprocta* are longer anteroposteriorly than those of *Incamys*, but those of all three increase in transverse diameter and decrease in anteroposterior as wear proceeds; the lowers also do this, but to a less marked degree. No figured specimens of *Scleromys* have unworn teeth, but the teeth plainly show the S-configuration and are intermediate in length between those of *Incamys* and those of the living species (Scott, 1905: Pl. 65, Figs. 13–15). No other known extinct dasyproctid resembles the living species as closely as do these two in molar structure.

As concerns the skull, there are various resemblances between *Incamys* and the surviving forms. These are described in detail above. The more striking are the general shape of the skull in lateral view, the large orbits with their posteriorly situated postorbital processes, and the nearly parallel cheek tooth rows.

The resemblances are, of course, accompanied by an array of differences, as is only to be expected when comparing an early Oligocene form with living ones. The majority of these differences seem to be characters primitive for the Caviomorpha. In this category are: 1), the flatness of the cranial roof; 2), the relative shortness of the snout; 3), the more abruptly projecting anterior root of the zygoma; 4), the great posterior extension of the nasals and ascending processes of the premaxillaries; 5), the very large incisive foramina, the groove running back from them, and the associated wide separation of the fossae for the *Mm. buccinatores*; 6), the less arched occiput; and 7), the relatively slight dorsal extension of the supraoccipital at the center. Of these, 1) to 3) are present in *Cephalomys*, *Branisamys*, and *Platypittamys*; 4) occurs in *Cephalomys* and *Branisamys*, but not in *Platypittamys*. *Franimys* and *Protoptychus* have this character very well developed, however; *Platypittamys*—and the octodontoids generally—may have shortened these elements early. Character 5) is shared with *Cephalomys* and also with *Protoptychus*. *Platypittamys* is unknown as regards this character, but Santacruzian octodontoids possess it. *Branisamys* does not, and this is perhaps an early specialization. Characters 6) and 7) occur in *Platypittamys*, and are not known for the other Deseadan genera. In features in which *Scleromys* differs from *Incamys* (p. 426), it is intermediate structurally between the latter and the living species. Cranial evolution in the lineage leading to *Dasyprocta* and *Myoprocta* has involved a considerable lengthening of the skull that has not been accompanied by a proportionate increase in the length of the cheek-tooth row. Cheek-tooth length is nearly equal to snout length in *Incamys* (99%), less in *Scleromys* (86%), and still less in *Dasyprocta* (57%). The palate of *Scleromys* is relatively wider and longer than in *Incamys*, relatively narrower and shorter than in *Dasyprocta*, and, as in the latter, lacks the anterior groove.

Incamys is distinguished, among known dasyproctids, by the relatively very large, posteriorly expanded bulla and those features related to it, namely the narrowness of the anterior portion of the basioccipital, the slight degree of inflation posterodorsal to the tympanic,

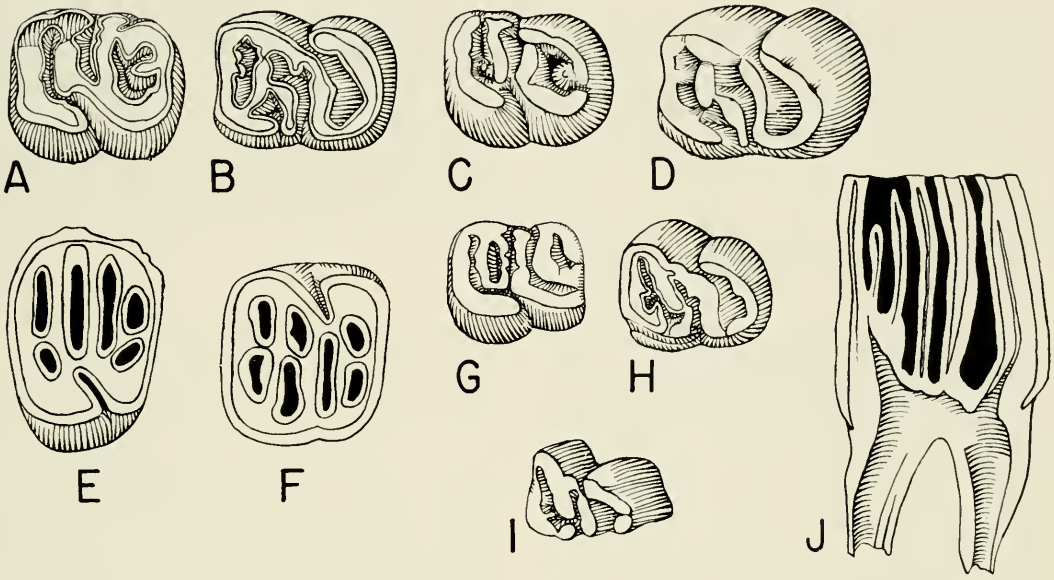

Figure 20. Molars of *Dasyprocta* and *Myoprocta*, ×5. A–D. *Dasyprocta noblei*, MCZ no. 15937. A. Worn LM^1. B. Worn RM_1. C. Unerupted LM^2. D. Unerupted RM_2. E–F. *Dasyprocta punctata isthmica*, MCZ no. 36361. E. LM^2. F. RM_2. G–I. *Myoprocta acouchy*. G. MCZ no. 30808, erupting LM^2. H. MCZ no. 30808, erupting RM_2. I. MCZ no. 30805, unerupted RM_3. J. Vertical section of (unspecified) lower molar of *Dasyprocta croconata*, redrawn from Hagmann, 1907, Pl. 26, Fig. 9. Anterior end to the left.

and, possibly, the short, non-projecting paroccipital process. This is partly a function of size. A large bulla tends to be characteristic of small rodents; in *Platypittamys*, for example, it is large although not so expanded posteriorly. (*Protoptychus* has an even larger bulla that is more posteriorly expanded and accompanied by a much greater degree of inflation in areas dorsal and posterodorsal to it; it may well have been a saltatorial adaptation.) The large size of the bulla would not rule *Incamys* out as an ancestor of the living dasyproctids, but the posterior expansion and the neighboring slight inflation are features of which not a trace is to be seen in *Dasyprocta* and *Myoprocta*. These, the presence of a "posterior postorbital process," and the peculiar interorbital fenestra incline us to suspect that while *Incamys* was close to the *Dasyprocta-Myoprocta* lineage, it lay a little to the side of it. Whether *Scleromys* was a descendant of *Incamys* or was more nearly on the main line are questions that only future discoveries can answer.

Knowledge of the upper dentition of *Incamys* permits the identification of an isolated left upper cheek tooth from the Deseadan of Patagonia that we described earlier (1959: 362, Fig. 24) as ?Dasyproctidae gen. et sp. indet. This is so close in details of structure to P^4 of *I. bolivianus*, especially to that of PU no. 21728 (Fig. 17B), as to leave no doubt at all as to generic identity, and on the evidence we cannot separate it specifically from the Bolivian species. We had previously been in some doubt as to the position of this tooth in the series, suspecting that it was too molariform in structure for a Deseadan premolar on the basis of the Patagonian evidence then available. The new Bolivian evidence conclusively shows that at least in the Dasyproctidae and Dinomyidae quite molariform premolars had evolved by Deseadan time. We thus have two rodents of this Age in common

between Bolivia and Patagonia, now that *Cephalomys* has been recorded from Salla. The latter is the commonest mammal in the Patagonian Deseadan, as *Incamys* may well be in the Bolivian.

Undescribed Genus, Dasyproctidae aff. *Neoreomys*
Incamys bolivianus Lavocat, 1976, in part (*nec* Hoffstetter and Lavocat, 1970)

An incomplete right maxilla with erupting P^4 and little worn M^{1-2}, SAL 118, was identified as *I. bolivianus* by Lavocat (1976: 43–44, 45; Fig. 4B; Pl. 4, Fig. 2). He noted various differences from the mine run of specimens of that species, but regarded them as probably characterizing "une variété intraspécifique." The distinctions strike us as being of considerably higher taxonomic importance. Five, not four, lophs are present on the molars (see Fig. 1, p. 376), and the protoloph is joined to the apex of the protocone in the unworn P^4, both of which rule out reference to *Incamys*. Our series of *I. bolivianus*, considerably larger than that available to Lavocat, contains no specimen similar to SAL 118, nor any that are intermediate between it and typical *Incamys*.

The depths of the flexi and fossettes together with the early union of the protoloph and hypocone in the molars and the presence of a hypocone on P^4 forbid reference to *Cephalomys*. We are dealing, it would appear, with a hitherto unknown form. Of known dasyproctids it is closest to *Neoreomys* in molar structure, the only differences of any consequence being the more continuous, less interrupted lophs and the smaller size of the spur on the anterior slope of the posteroloph, which does not extend to the fourth crest, the neoloph (cf. Lavocat's stereophotograph with Wood and Patterson, 1959: Fig. 17A). The premolar differs in that the lophs are less obliquely directed relative to the long axis of the tooth row (cf. Scott, 1905: Pl. 65, Figs. 1–2), and a well-defined hypocone is present. The paracone sends a short spur linguad that would unite with the protoloph after very little wear; this could be an individual peculiarity.

On the scanty evidence available, we have, in SAL 118, a form that may have been close to the *Neoreomys* lineage, although not on the direct line to that genus.

Cephalomys Ameghino 1897
Cephalomys bolivianus Lavocat 1976

Cephalomys bolivianus Lavocat, 1976: 59–62; Fig. 3A; Pl. 6, Figs. 1–2.

Cephalomys, the commonest Patagonian Deseadan genus, is represented, with certainty, by one Bolivian specimen in the collection deposited in the Muséum Nationale. The type, SAL 164, consists of the ventral portion of a rostrum and most of the palate with the base of the incisor and deeply worn P^4–M^2 of both sides. As noted by Lavocat, the dimensions of the teeth fall within the size range of *C. plexus*, the smaller of the two previously known species. He gives (1976: 59) as diagnostic features the wedge shape ("en coin") of the rostrum, the very slight degree of posterior divergence of the cheek-tooth rows and the absence of an infraorbital groove.

The first two of these characters—and the smaller size—distinguish SAL 164 from *C. arcidens*, the type species. The rostrum is unknown in *C. plexus*, but the tooth rows are more divergent than in the Bolivian specimen. The reported absence of the groove (presumably for the infraorbital nerve and blood-vessels) may be more apparent than real. This is shallow in *C. plexus*, in which it is bounded laterally by a slight elevation on the side of the maxilla (Wood and Patterson, 1959: Fig. 22A). So far as can be judged from Lavocat's illustration, the type of *C. bolivianus* may have suffered some abrasion in this area, sufficient perhaps to have removed a comparable elevation had one been present. We are by no

means certain that *C. bolivianus* is not a synonym of *C. plexus*, but accept it provisionally.

As noted above, the rarity of *Cephalomys* in the Bolivian Deseadan is in striking contrast to its abundance at certain Patagonian localities, precisely the reverse of the situation as regards *Incamys*.

Dasyproctidae *inc. sed.*

Genus indet., Lavocat, 1976: 68; Pl. 5, Figs. 4–5.

Two mandibular fragments, one (SAL 166) with deeply worn M_{1-3}, the other (SAL 167) with badly broken P_4–M_2, were figured and described by Lavocat, who noted some resemblances to *Cephalomys*. There is indeed a certain similarity to teeth of that form at comparable stages of wear, particularly as regards the preserved posterior portion of P_4 (cf. Lavocat, 1976: Pl. 5, Fig. 5 and Wood and Patterson, 1959: Fig. 18B). The molars of SAL 166 are so deeply worn that the mesoflexids are represented only by undulations on the lingual surfaces, yet a minute remnant of the anterofossettid of M_2 and of the metafossettid of M_3 still remain. In the Patagonian species of *Cephalomys* all traces of these would have been lost at much earlier stages of wear.

It is conceivable that these specimens might be referable to *C. bolivianus*, with which they agree in size, but it is impossible to be certain on such material.

Family DINOMYIDAE Alston 1876
Branisamys Hoffstetter and Lavocat 1970

Synonym. Villarroelomys Hartenberger 1975.

Emended Diagnosis. Skull, so far as known, basically dinomyid. Snout heavy, ventral side of rostrum elevated as in some dinomyids, less so than in *Dinomys*; fossa for origin of *M. masseter medialis, pars anterior* very deep, markedly excavated dorsally; nasals wide anteriorly, tapering gradually posteriorly, longer than in *Dinomys*, extending back over M^1. Posterior ends of nasals and premaxillae forming nearly straight line across top of skull. Interpremaxillary foramen half way back on mid-ventral surface of premaxilla, small, round, not slit-like. Premaxillary-maxillary suture crossing palate at rear of short, broad incisive foramina. Strong vertical ridge near front of lacrimal. Posterior palatine foramina beside M^1, entirely within palatine. Anterior end of palatine reaching forward to posterior end of P^4. Posterior margin of palate with small median process as in Paramyidae and Reithroparamyidae. Cheek-tooth rows divergent posteriorly. Knob for *M. masseter superficialis* on ventral surface of zygoma, as in *Dinomys*. Dental formula I_1^1, P_1^1, M_3^3, dm_1^2; incisors with flat anterior faces, robust but smaller and narrower relative to cheek teeth than in later dinomyids, gently rounded anteriorly. Base of upper incisor above P^4. Single rooted dm^3 present; dm^4 and P_4^4 essentially molariform, P^4 with low metaloph; dm_4 with highly complex anterior portion. Cheek teeth low crowned with incipient unilateral hypsodonty, lingual in upper teeth, labial in lowers. Cheek teeth slightly longer than wide when little worn, becoming wider than long with wear. Anteroloph of upper cheek teeth isolated in early stages of wear; remaining lophs uniting early and converging posterointernally on hypocone. Lower cheek teeth with posterolophid isolated in early stages of wear, remaining lophids uniting early and converging anteroexternally on protoconid.

Type Species. Branisamys luribayensis Hoffstetter and Lavocat 1970.

Distribution. Deseadan Oligocene of Bolivia.

Branisamys luribayensis Hoffstetter and Lavocat 1970
Figures 21–25

Synonym. Villarroelomys bolivianus Hartenberger 1975.

Diagnosis. As for the genus. Tooth measurements as given in Tables 5–6.

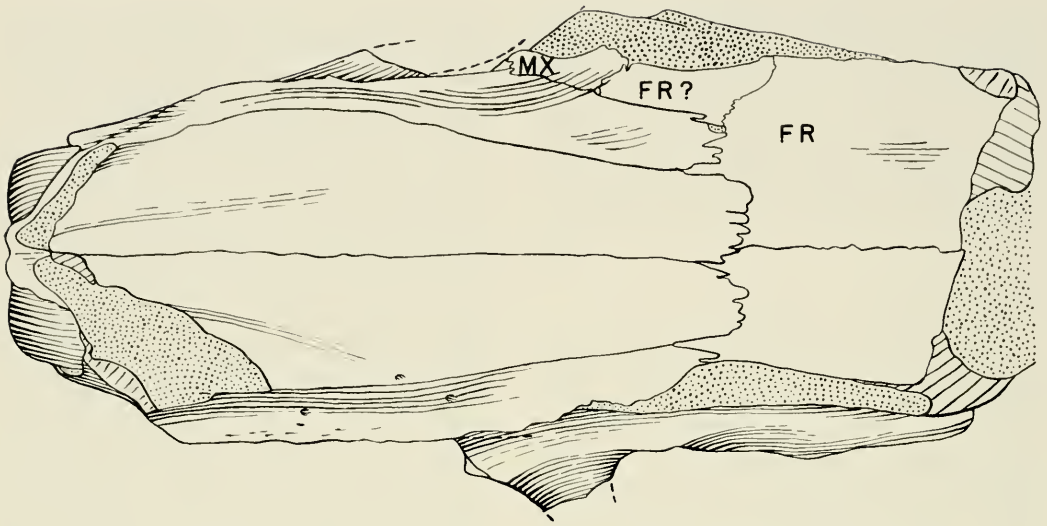

Figure 21. Dorsal view of skull of *Branisamys luribayensis*, PU no. 20914, ×3.

Abbreviations: FR—frontal; FR?—probable process of frontal, with crack between it and frontal; MX—ascending process of maxillary. Dotted areas are matrix.

Type. Portion of skull with root of dm^3, dm^4–M^3 right, cited without museum number or museum location by Hoffstetter and Lavocat (1970: 172), and as SAL 102, without museum designation, by Lavocat (1976: 33).

Type of Synonym. An incomplete Ldm_4, GB 014.

Referred Material. 31 specimens in the MNHN and Princeton collections, listed in Appendix 1 (p. 528).

Horizon and Locality. Deseadan early Oligocene, lower part of Estratos de Salla; Salla-Luribay Basin, Bolivia; all specimens are from near Salla Farm.

Description. The type is a skull missing the snout, the zygomatic arches, the occiput and part of the basicranium. Unfortunately, it has not been prepared enough to show any of the basicranial features or those of the orbit. Lavocat (1976: 34) stated that the orbitotemporal region is poorly preserved; his stereophotos (Pl. 2, Figs. 1, 3) suggest that it is still buried in matrix. Unfortunately, sutures are often impossible to identify on the photos. The Princeton skull, PU no. 20914, therefore adds considerably to our knowledge of the genus.

The rostrum is short—the length of the diastema being approximately equal to that of the cheek-tooth row (Figs. 22, 23A)—and very stout, comparable to those of *Neoreomys* and *Dinomys*, and much more robust than those of *Platypittamys*, *Cephalomys*, *Incamys* or the living dasyproctids. Dorsally, the sides are nearly parallel for most of their length but are slightly convergent anteriorly (Fig. 21); ventrally, they converge forward from the anterior roots of the zygomatic arches (Fig. 23A). The ventral surface is wide, gently rounded in the premaxillary portion and slightly concave in the maxillary portion anterior to the cheek teeth; this is probably the fossa of origin of *M. maxillolabialis*. As may be seen in side view (Fig. 22), the under side of the rostrum slopes steeply upward relative to the occlusal surface of the

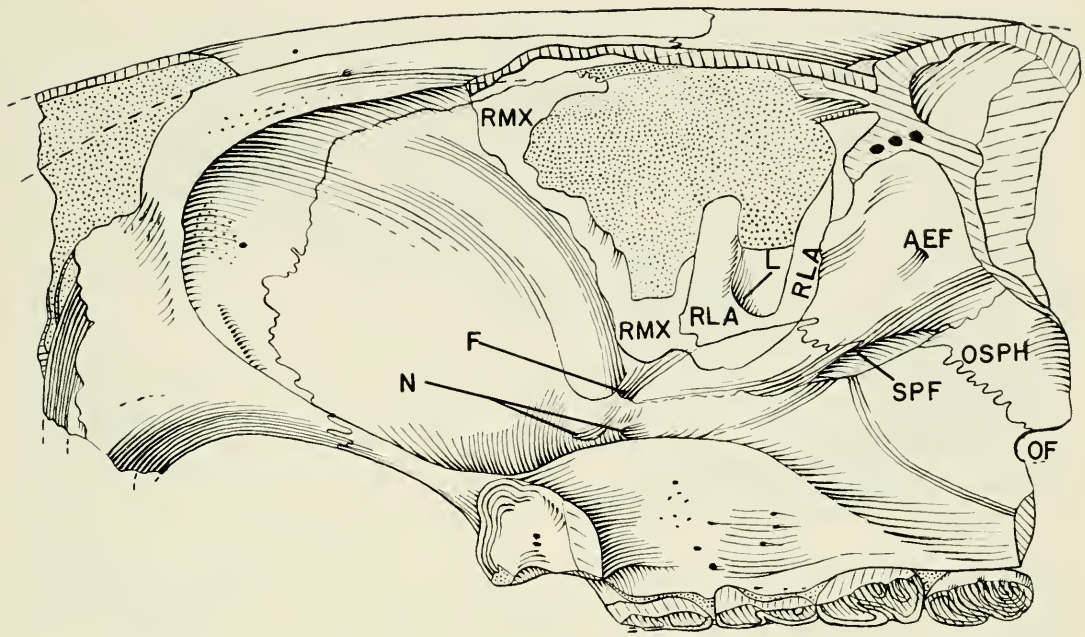

Figure 22. Lateral view of skull, *Branisamys luribayensis*, PU no. 20914, ×3. Part of orbital region restored from right side.

Abbreviations: AEF—anterior ethmoid foramen; F—foramen into nasolacrimal canal; L—lacrimal foramen; N—nutritive foramina; OF—optic foramen; OSPH—orbitosphenoid; RLA—right lacrimal, reversed from opposite side; RMX—part of right maxillary, reversed from opposite side; SPF—sphenopalatine foramen. Dotted areas are matrix.

cheek teeth, not so much as in *Dinomys* but in striking contrast to the condition in the dasyproctids. Most of the lateral surface of the snout is occupied by the very large fossa for *M. masseter medialis, pars anterior*, which extends far forward onto the premaxilla. The fossa is comparable in extent, except anterodorsally, to that of *Dinomys* but is more deeply incised and is bounded anteriorly and dorsally by a much more prominent bony rim (Fig. 22).

As in *Incamys*, the nasals are very long for caviomorphs, extending back to a point above M^1. In *Branisamys* these bones are narrow. Bluntly pointed, they increase somewhat in width posteriorly for slightly less than half their lengths and then decrease evenly toward the frontals. In contour, therefore, they resemble the shorter and wider nasals of *Dinomys*, and differ from the posteriorly tapering ones of *Neoreomys* or the more parallel-sided ones of *Incamys* and the living dasyproctids.

The premaxillaries are large and robust. Ventrally, they are relatively wider and the lateral margins are more convergent anteriorly than in *Dinomys* and, as already noted, they are more excavated laterally for the reception of the anterior portion of *M. masseter medialis*. The incisive foramina are kidney-shaped (Fig. 23A), much broader in proportion to length than in *Dinomys* or the living dasyproctids; in contrast to *Incamys* and others (p. 400), they do not extend posteriorly. The interpremaxillary foramen is small, positioned as in *Dinomys*, but is round, rather than elongate as in the living genus or in *Neoreomys*. The premaxillary-maxillary suture crosses the palate

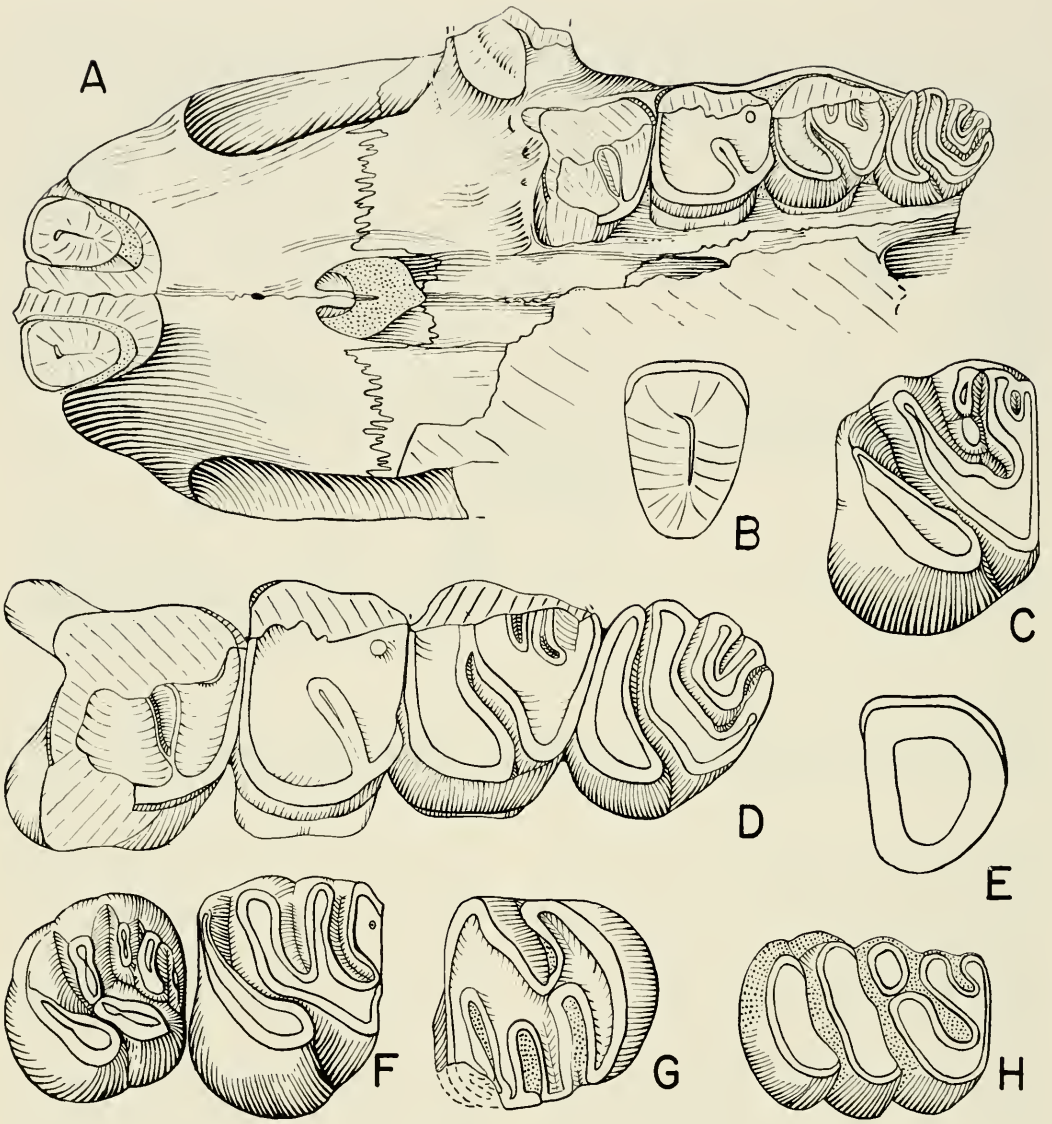

Figure 23. Skull and teeth of *Branisamys luribayensis*, and tooth of *Dinomys*. Skull, ×3, teeth, ×5. A. Ventral view of skull, PU no. 20914. Dotted areas are matrix. B. LI^1, PU no. 20914, from the front. C. LP^4, PU no. 20915. D. LP^4–M^3, PU no. 20914. E. RI_1, PU no. 21734, from the front. F. LP^4–M^1, PU no. 21732. G. RM_3, PU no. 21734. Dotted area is matrix. H. *Dinomys* sp., LM^1, AMNH (Mam.) no. 100011. Dotted areas are cement.

at the rear of the incisive foramen, then bends forward along the lateral margin of the foramen to its middle, where it turns transversely laterad across the palate, turns dorsad on the side of the snout, though with somewhat of a forward bulge that is reminiscent of the paramyids and reithroparamyids (e.g., Wood, 1962a: Figs. 2B, 13B, 48B). The positioning of the suture along the ventral surface is very like that in *Dinomys*. The dorsal process of the premaxillary extends back

almost as far as the posterior end of the nasal (Fig. 21).

As in *Dinomys*, there are paired gutters along the palate, running from the incisive foramina to the posterior palatine foramina. The two gutters are separated, again as in *Dinomys*, by a median ridge, but one much lower than in the living genus. The palate narrows forward (or the cheek tooth rows converge) as in *Dinomys*. The posterior palatine foramina lie in the gutters, as in *Dinomys*, but the foramina are in the palatine, whereas in *Dinomys* they are on the maxillary-palatine suture. Our description of this area differs slightly from that of Lavocat (1976: 35). We cannot determine whether this is due to variability of this area in *Branisamys*, or whether his description is in error, since we found it impossible to trace the maxillary-palatine suture on his stereophotos (Lavocat, 1976: Pl. 2, Figs. 1, 4). Posterior to the foramina, the maxillary forms a shelf, lateral to the palatine and separating it rather widely from the alveoli of the molars.

There is a prominent rugosity for the tendon of *M. masseter superficialis* at the medial end of the zygoma. To judge from conditions in the Paramyidae and Reithroparamyidae (Wood, 1962a: Figs. 24C, 31C, 48B), this is a primitive character. As in *Dinomys*, the passage for the infraorbital nerve and blood vessels is crowded between the base of the incisor and the root of the zygomatic arch. There are two fair-sized nutritive foramina in the ventral wall of this passage (Fig. 22; N). The sphenopalatine foramen lies in the posterior part of the orbital portion of the maxilla and is touched posteriorly by the orbitosphenoid and bounded along its posterodorsal portion by the frontal. On the left side, a valley for a nerve or blood vessel runs ventrally and then posteriorly from this foramen (Fig. 22). No trace of this channel was detected on the right side.

In *Dinomys*, a small opening in the maxillary, just behind the root of the incisor, opens into the nasolacrimal canal, as can be seen by passing a flexible probe through the canal from the lacrimal foramen. This opening is very much smaller than in the later dasyproctids. There is a foramen, in *Branisamys*, just behind and below the base of the incisor, from which a faint groove extends upward and backward toward the lacrimal foramen (Fig. 22; F). Breakage on the right side shows that this foramen is continued forward in the bone, toward the nasal passage, and that it unites with another channel, running in the same general direction, which appears to be the nasolacrimal canal. This foramen would seem, then, to be homologous to the opening in *Dinomys* and to the much larger one of the later dasyproctids.

The fragmentary snout (PU no. 21960) is broken, anteriorly, at about the midpoint of the upper incisors (Fig. 25B). The incisors, inclosed in the premaxillae, have a large pulp cavity. Ventrally, the incisive alveolus is separated by a thin lamella of bone from a rounded cavity, the anterior extension of the nasolacrimal canal (Figs. 24A, 25B; NLC). The ventral portion of the premaxilla bears a V-shaped dorsal groove that houses the vomer (Fig. 25B). Between the incisive alveoli, there are at least two vertical lamellae of bone, probably portions of the turbinals, above which the nasal cavity widens (Fig. 25B; NC).

Seen from the side (Fig. 24A), the most important feature of this fragmentary snout is the nasolacrimal canal, which passes forward and ventrally from the lacrimal foramen, ventral and mesial to the base of the incisor and lateral to the nasal passage. At about the middle of the fragment, the canal enlarges and curves upward (Fig. 24A) to form a large, rounded cavity just ventral to the incisive alveoli, as seen from the front (Fig. 25B; NLC). Posteriorly, the snout is broken off just behind the cribriform plate, so that this latter is exposed from the rear. The plate is about 8.5 mm wide and 7 mm high.

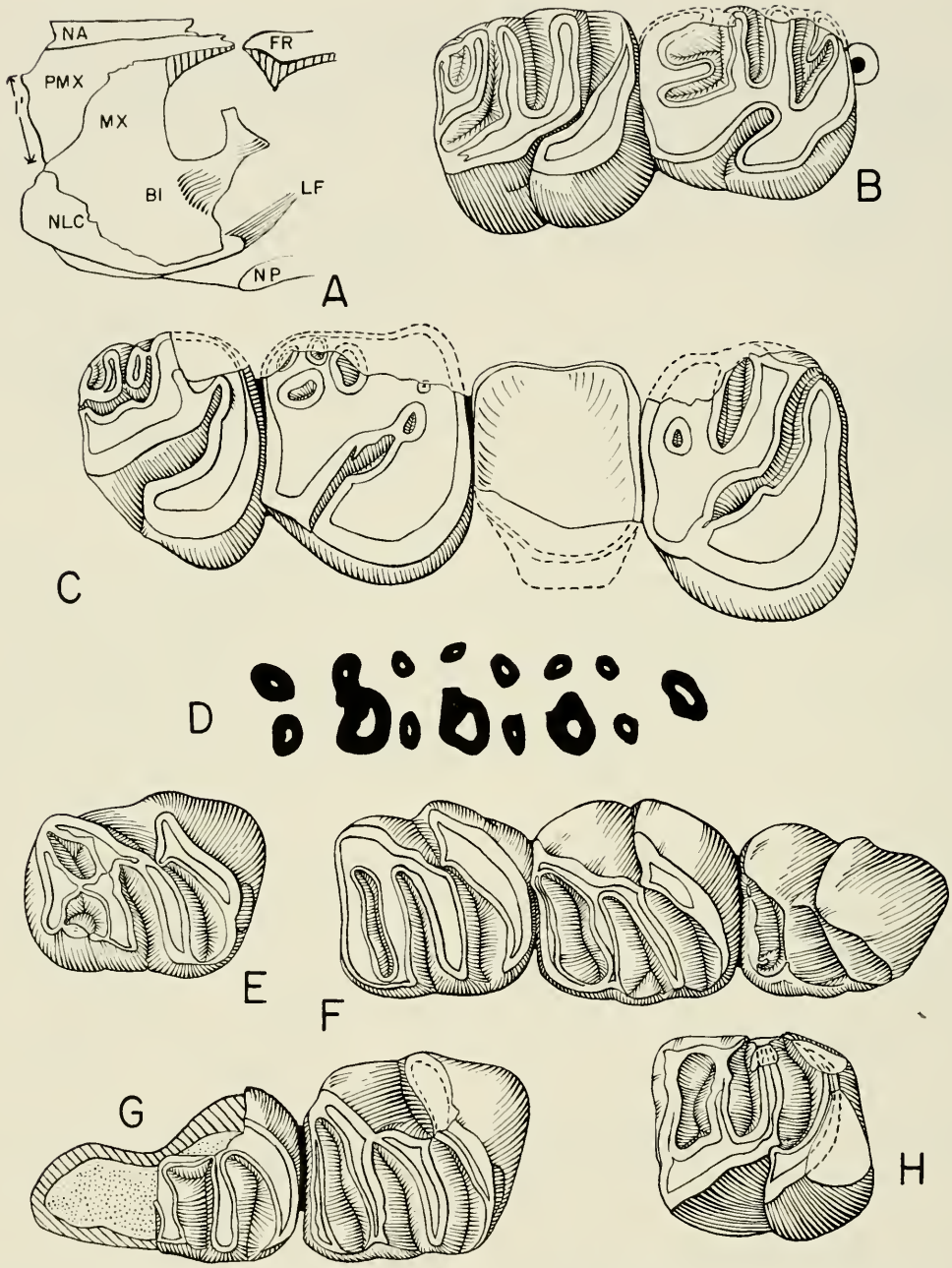

Figure 24. Snout and teeth of *Branisamys luribayensis*. Teeth, ×5; other scales as indicated. A. Ventrolateral view of snout, PU no. 21960, oriented with dorsal surface of nasal horizontal, ×2. B. PU no. 21955, Rdm^4–M^1 and root of dm^3; anterior end to the right. C. PU no. 21943, RP^4–M^3, anterior end to the right. D. Root pattern of PU no. 21978, edentulous lower jaw, ×3. E. PU no. 21980, RP_4. F. PU no. 21944, RM_{1-3}. G. PU no. 21987, broken Rdm_4 and M_1. H. PU no. 21986, LM_2.

Abbreviations: BI—base of incisor; FR—frontal; I^1—position of upper incisor; LF—lacrimal foramen; MX—maxilla; NA—nasal; NLC—nasolacrimal canal; NP—nasal passage; PMX—premaxilla.

There are relatively few, rather large olfactory foramina. There is a well-developed lamina perpendicularis, on either side of which is an elongate vertical opening.

The nasofrontal sutures are irregular; the frontals notch the nasals very slightly at the midline, and send forward small wedges between the premaxillaries and nasals (Fig. 21), as in *Cephalomys*. The Princeton specimen does not extend far enough posteriorly to determine whether or not a postorbital process was present, but one clearly was present in the type (Lavocat, 1976: 34; Pl. 2, Fig. 3). On the right side of the skull of PU no. 20914 there is a piece of bone (Fig. 21; FR?) lateral to the premaxilla and abutting anteriorly against the maxilla, from which it is separated by an obvious suture. Posteriorly, this section is separated from the frontal by either a suture or a very suture-like crack. Unfortunately this area is missing on the left side, as well as on the type. If this area is part of the frontal, as seems likely, then a projection from that bone extended forward between the premaxilla and maxilla as in *Cephalomys*, *Incamys*, and the living dasyproctids. If, on the other hand, this area is not part of the frontal but some other ossification (most likely a peculiarly shaped dorsal process of the lacrimal), the anterior edge of the frontal is almost exactly as in *Dinomys* and *Neoreomys*.

Much of the orbital portion of the frontal is present on the right side of PU no. 20914, and agrees closely, so far as preserved, with the corresponding part in *Dinomys*, being much less concave in the anteroposterior direction than in the living dasyproctids or *Neoreomys*. The ventral margin of the frontal forms a nearly horizontal line, running back from the posteroventral corner of the lacrimal to the orbitosphenoid. A good-sized anterior ethmoid foramen enters the frontal, in a posterodorsal direction, above M^3. This area has not been prepared in the type (Lavocat, 1976: Pl. 2, Figs. 1, 3).

The ventral half of the right lacrimal is present; it is very similar to that of *Dinomys*, being essentially flat and lacking any trace of the vertical plate that, in dasyproctids, connects the cranial and preorbital portions of the bone and buttresses the dorsal root of the zygomatic arch. A vertical ridge near the front of the lacrimal of *Branisamys* marks the anterior margin of the lacrimal gland just above the nasolacrimal canal. Such a ridge does not occur either in *Dinomys* or in the dasyproctids, unless, perhaps, the ridge is homologous to the initial development of the buttress of the dasyproctids.

The anterior end of the palatine, at the midline, reaches the level of the rear of P^4, a condition that is more dasyproctid than dinomyid. According to Lavocat (1976: 35) the palatines of the type reach only to the anterior quarter of M^1. The notch at the rear of the bony palate is rounded in Lavocat's figure of the type (1976: Pl. 2, Fig. 4), and lies opposite the middle of M^2; in PU no. 20914 (Fig. 23A) it clearly curved across the palate farther posterad, and there are the remains of what seems to have been a median tubercle (Fig. 23A) as in the Paramyidae, Reithroparamyidae, and *Neoreomys*, a structure not present in *Dinomys* or living dasyproctids.

The little that is preserved of the orbitosphenoid reveals that, anteriorly, it reached the posterior margin of the sphenopalatine foramen (Fig. 22), as in *Incamys* and modern dasyproctids and in contrast to the condition in *Dinomys*, and that the optic foramina were close together and confluent as in *Dinomys*, *Incamys*, and modern dasyproctids, whereas the two foramina are widely separated in *Neoreomys*.

The posterior part of the frontals and the parietals, together with the available parts of the squamosal and bulla, have been described by Lavocat (1976: 34–35).

As stated by Lavocat (1976: 35), the mandible is heavy. It is, however, not "extrêmement" robust as stated by Lavo-

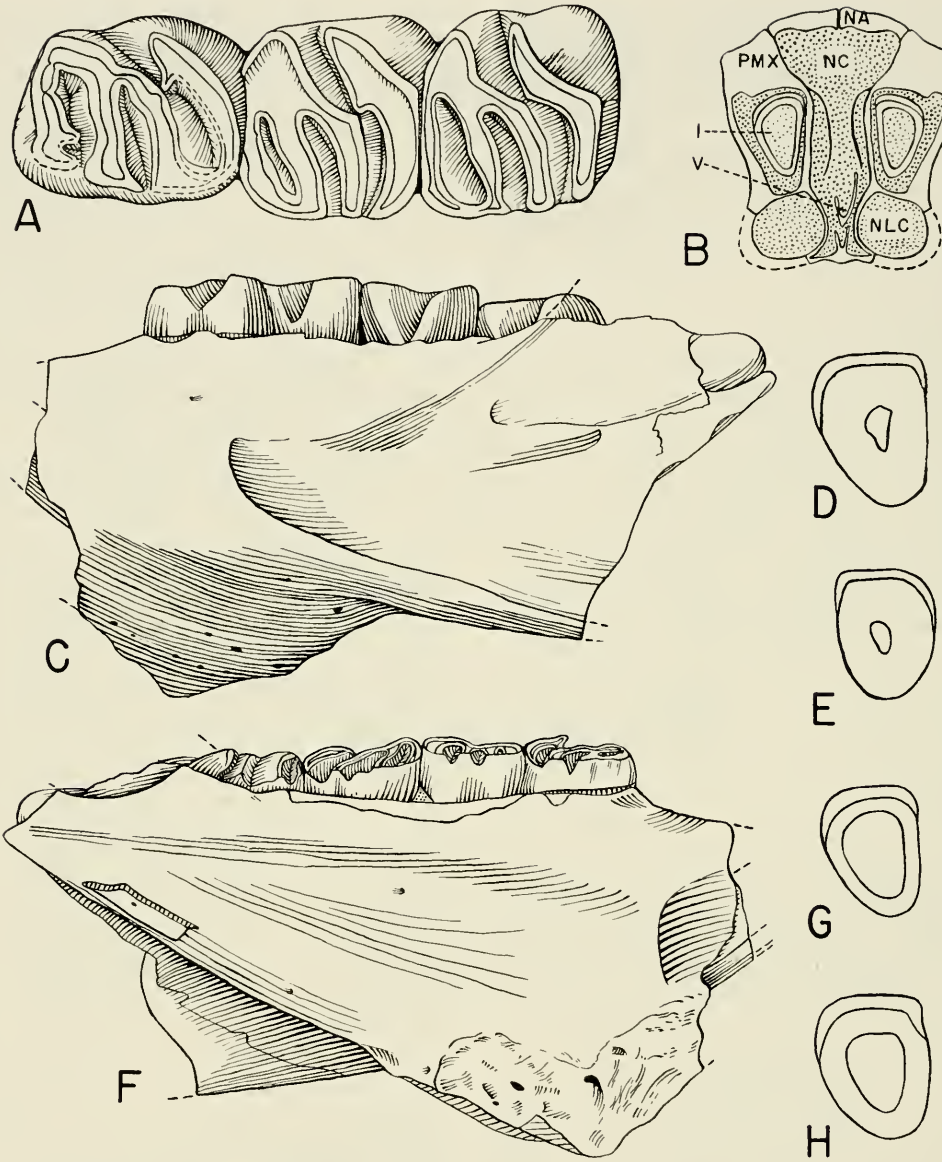

Figure 25. Snout, jaws and teeth of *Branisamys luribayensis*. Teeth, ×5; other scales as indicated. A. PU no. 21951, RP_4–M_2. B. PU no. 21960, snout broken about mid-length, seen from front. C. Lateral view of lower jaw, ×3. Largely based on left mandible, PU no. 21978, but masseteric fossa and angle completed from PU no. 21979; teeth reversed from PU nos. 21944 and 21951. D. PU no. 21978, cross section of LI_1 below diastema. E. PU no. 21944, cross section of RI_1 below anterior root of dm_4. F. Medial view of lower jaw, ×3. Based on same specimens as in C. G. PU no. 21987, cross section of RI_1 below rear of M_1, seen from the rear. H. PU no. 22172, cross section of RI_1 below rear of M_2, seen from the rear.

Abbreviations: I—cross section of incisor; NA—nasal; NC—nasal cavity; NLC—nasolacrimal canal; PMX—premaxilla; V—vomer. ×2.

cat, nor anywhere near so heavy as it would appear in his figures (1976: Pl. 2, Figs. 5–7), in which the jaw was photographed perpendicular to the occlusal surface. As in all caviomorphs, if the jaw is oriented in its natural position, the occlusal surface of the cheek teeth slopes down at about 30° toward the midline. When photographed perpendicularly to the occlusal surface, the medial surface of the jaw, which was vertical in life, appears as a broad medial shelf (Lavocat, 1976: Pl. 2, Figs. 5–7). Anteriorly, our specimens are all broken farther to the rear than is SAL 105 (Lavocat, 1976: Pl. 2, Fig. 6) and show nothing of the length of the diastema (Fig. 25C,F). However, his photograph looks as though the incisor had been pushed to the rear in SAL 105, greatly shortening the diastema. There is a deep and very narrow groove on the ventral surface of the mandible between the incisive alveolus and the angular process, which seems to differ from what Lavocat saw, since he said (1976: 35) that the groove was "large et profond." However, his stereophoto (1976: Pl. 1, Fig. 6) shows that the matrix had not been removed from this region before the specimen was photographed. There is a prominent chin process (Fig. 25C) on which there are a number of nutritive foramina. There is no trace in any of the Princeton specimens of a mental foramen (Fig. 25C; the small foramen beneath P_4 in PU no. 21978 faces backward and cannot be a normal mental foramen), which would seem to indicate that the foramen was farther forward than in *Dinomys* (Ellerman, 1940: Fig. 41). Lavocat neither figures nor mentions a mental foramen. The dorsal border of the masseteric fossa is clearly marked and is continued into the coronoid process, which passes the alveolar border by the talonid of M_3. There are a number of suggestions of subdivision within the masseteric fossa (Fig. 25C), among which the insertion of *M. masseter medialis, pars posterior* (Woods, 1972: 128, Fig. 3A) is the most prominent.

On the medial surface of the mandible, the chin process, behind the symphysis, is highly corrugated (Fig. 25F). There is a distinct cavity, above the corrugated area and in front of P_4, which may represent the fossa for an unusually large *M. genioglossus*. This view of the jaw shows the position of the deep groove between the incisive alveolus and the angular process.

At the time of its description, the type provided, for the first time among Deseadan caviomorphs, some evidence of the upper deciduous dentition (Hoffstetter and Lavocat, 1970: Fig.; Lavocat, 1976: 36, Pl. 2, Fig. 4), but it is no longer unique, as the upper deciduous dentition of *Incamys* is now known (see above, p. 425) and dm^4 and the root of dm^3 of *Branisamys* are present in PU no. 21955 (Fig. 24B). This specimen and the type preserve the single root of a very small tooth in front of dm^4 (for a discussion of the precise nature of the tooth in front of dm^4 or P^4, see Wood, 1969; 1970b: 245–246). In the adult Princeton specimens there is no trace of such an alveolus, the maxilla sloping upward from the anterior border of the alveolus of P^4 with no indication of an anterior alveolus, unless what seem, in PU no. 20914, to be nutritive foramina represent the last stage in the filling of the alveolus with replacement bone, as occurs in the European paramyid *Plesiarctomys* (Wood, 1970b: 245, Fig. 8), and, possibly, in *Sallamys* (p. 383). However, there are definite nutritive foramina in this position in, e.g., *Erethizon*, in which neither dm^3 nor P^3 is ever present (Wood and Patterson, 1959: 378). The areas in front of P^4 in PU nos. 20915, 21732, 21733, and 21943 show no nutritive foramina and no suggestion of an alveolus.

The functional upper cheek teeth are basically low crowned, although unilateral hypsodonty has begun to develop on

TABLE 5. MEASUREMENTS, IN MM, OF UPPER TEETH OF *Branisamys luribayensis*.

PU nos.	20914 L	20914 R	20915 L	21732 L	21733 R	21943 R	21955 R	21960 L	N	$\bar{X}$
P^4–M^3 anteroposterior	20.8					20.9			2	20.85
dm^4 anteroposterior							5.83		1	
width metaloph							5.00		1	
P^4 anteroposterior	5.20		5.50	4.68	4.53	5.53			5	5.09
width protoloph			6.82	5.18	5.05	7.30			4	6.09
width metaloph			6.29	5.24	6.15				3	5.89
M^1 anteroposterior	4.34			4.88	4.85	4.45	5.40		5	4.78
width protoloph	ca. 5.9			6.45	6.30		5.92		4	6.14
width metaloph				5.83	5.40		5.83		3	5.69
M^2 anteroposterior	5.05					5.57			2	5.31
width protoloph	ca. 6.0								1	6.0
M^3 anteroposterior	4.82					4.98			2	4.90
width protoloph	5.44								1	5.44
width metaloph	5.30					5.14			2	5.22
I^1 anteroposterior	4.9							4.21	2	4.56
transverse	3.32	3.24						3.14	3	3.23
ratio	.68							.75	2	.71

the lingual side. Lavocat (1976: 36) compares this condition to that in the Miocene *Paraphiomys pigotti* of Africa. There is no question but that the two are at comparable stages of evolution of unilateral hypsodonty. However, the same may be said for many other rodents (paramyids, reithroparamyids, theridomyids, prosciurines, ischyromyids and cylindrodonts, to name a few selected at random from the early Tertiary). All that this indicates is that unilateral hypsodonty is very common in the upper cheek teeth of rodents—and lagomorphs as well (Wood, 1942: 4, Table p. 5). Unilateral hypsodonty has absolutely no weight as an indication of caviomorph-thryonomyoid relationships short of the ordinal level. The degree of lingual hypsodonty in *Branisamys* is no greater, proportionately, than in most paramyids and reithroparamyids. Enamel was continuous around the crown until late stages of wear (Figs. 23D, 24C, rear of M^1), and there does not seem to have been very much interdental wear. The teeth are somewhat wider than long for most of their lifetime, but in the early stages of wear the grinding surfaces are rather longer than wide (Table 5). This change takes place through the progressive widening of the wear surface down the lingual slope of the protocone and hypocone, but the change is not so prominent as in *Incamys*.

All upper cheek teeth are five-crested (Figs. 23C,D,F; 24B,C; Lavocat, 1976: Pl. 2, Fig. 4), having a small fourth crest, the neoloph, that attaches to the anterior face of the fifth crest, the posteroloph, near its middle. For terminology of the parts of the cheek teeth, see Figs. 1–2 (pp. 376–377). Each tooth overhangs posteriorly behind the hypoflexus, which results in progressive decrease in the size of the posterointernal corner as wear proceeds. There is a slight tendency for the enamel to be thicker on some of the anterior than on some of the posterior faces of the lophs, a tendency carried much farther in *Dinomys*. Cement is lacking on all teeth.

Little worn teeth are preserved in PU nos. 20915, 21732, 21733, 21943 and 21955. P^4 is almost, but not quite, fully molariform. Protocone and anteroloph together form a stout crest, bulging anterolingually (Fig. 23C,F), that extends from the posterolingual portion of the crown around most of the anterior face, falling

short of the paracone. Paraflexus and hypoflexus are confluent through much of the depth of the crown, effectively isolating this anterior crest until an advanced stage of wear (Figs. 23A, 24C). The protoloph, thus separated from the protocone, extends obliquely from the paracone to the hypocone. In early wear stages (Fig. 23F) the two cusps are separate. The mure, as such, has lost all individuality. The neoloph is a short crest that joins the center of the posteroloph after a little wear. Labially, it soon fuses with the posteroloph to isolate a small, ephemeral neofossette. The "metaloph" is the last of the crests to come into wear. Although we employ the same names for structures on premolars as for the topographically corresponding ones on the molars, it is nevertheless quite clear that the metaloph has had different histories in the two sets of teeth (p. 386). It is closest to the wear surface labially where it approaches the neoloph, from which it is separated by a slight notch, and then makes contact far dorsal to the grinding surface with a bulge on the labial side of the protoloph. Midway in its course, the metaloph is slightly constricted from below and from the sides, and these constrictions give it a fleetingly bicuspidate structure. The combined para- and hypoflexus and the mesoflexus extend to within short distances of the base of the enamel. The small neoflexus, which is open labially only in the earliest stages of wear (Fig. 23F), is the shallowest of the crown features, and disappears after a small amount of wear (Fig. 24C). This is the most advanced P^4 yet reported from Deseadan rodents. The premolars of PU nos. 21732 and 21733 have different measurements and are smaller than those of the other specimens (Table 5) because the teeth are not fully erupted.

The molars differ from P^4 primarily in the more buccal extension of the anteroloph, in their greater length on eruption (Fig. 24B) and in the more nearly central position of the lingual opening of the hypoflexus, again on eruption (Fig. 24B). The length rapidly decreases with wear. The three posterior lophs are variable in their connections. M^1 and M^3 of the type resemble P^4 of PU no. 20915. In M^2 of the type, however, the central portion of the metaloph inclines posteriorly to unite with the neoloph, its normal course being marked by a buccal cuspule. This cuspule was regarded by Hoffstetter and Lavocat (1970) and by Lavocat (1976: 37) as a mesostyle. We take it to be a minor individual variant representing a secondarily isolated remnant of the metacone. Comparable metaconal isolations can be seen in little worn molars of *Dinomys*, as individual variations (Fig. 23H). The valley between the posteroloph and the neoloph is extremely shallow (Fig. 24B) and rapidly removed by wear (Fig. 23F).

In M^3 of PU no. 20914 (Fig. 23D), the metaloph and neoloph unite in an irregular V that is isolated from the protoloph and posteroloph by the combined mesoflexus and neoflexus; slight additional wear would result in a neoloph-posteroloph union. In PU no. 21943 (Fig. 24C), the posteroloph and neoloph have united, leaving a nearly isolated metacone. These variations are of no taxonomic significance; minor and inconsequential shiftings of loph connections occur with some frequency among caviomorphs. The molars of PU nos. 20914 and 21940, older individuals than the type, reveal that the combined paraflexus and hypoflexus closes from the buccal toward the lingual side, and that the metafossette is somewhat more persistent than the mesofossette. In the type, M^3 is small in comparison with the anterior teeth, which is not the case in PU nos. 20914 and 21943; this may be due to incomplete eruption of M^3 in the juvenile type. Lavocat's stereophoto (1976: Pl. 2, Fig. 4) suggests, however, that the eruption is almost complete but that the tooth is still partly buried in matrix.

There are a number of lower jaws in the Princeton collection, several being

TABLE 6. MEASUREMENTS, IN MM, OF LOWER TEETH OF *Branisamys luribayensis*.

PU nos.	21734 R	21944 R	21951 R	21978 L	21980 R	21986 L	21987 R	22172 R	22173 R	N	$\bar{X}$
P_4–M_3 anteroposterior				20.55 (alv.)						1	
dm_4 anteroposterior							ca. 7.15			1	
width hypolophid							ca. 4.7			1	
P_4 anteroposterior			6.13		6.28					2	6.20
width metalophid			4.58		4.29					2	4.44
width hypolophid			4.91		5.01					2	4.96
M_1 anteroposterior		5.17	4.64				5.40			3	5.07
width metalophid		5.02	5.26				5.37			3	5.22
width hypolophid		5.21	5.47				5.43			3	5.38
M_2 anteroposterior		5.56	4.80			5.67				3	5.34
width metalophid		5.50	5.46			5.55				3	5.50
width hypolophid		5.54	5.28			5.48				3	5.43
M_3 anteroposterior	5.67	5.63								2	5.65
width metalophid	5.63	4.74								2	5.19
width hypolophid	4.93	4.30								2	4.62
I_1 anteroposterior		3.47	4.03	4.08	4.55		3.48	3.80	4.00	7	3.92
transverse		2.65	2.92	3.07	3.66		2.65	3.04	3.17	7	3.02
ratio		.76	.73	.75	.80		.76	.80	.79	7	.77

edentulous, but the dentition is well represented by PU nos. 21944 (Fig. 24F); 21951; 21987 (Fig. 24G); 21980 (Fig. 24E); 21734 (Fig. 23G); and 21986 (Fig. 24H). The edentulous jaws clearly show the root pattern (Fig. 24D), with four well-separated roots (the largest beneath the hypoconid) on P_4–M_2, but with only a single anterior root under dm_4 and a single posterior one under M_3.

Lower teeth were illustrated by Hoffstetter and Lavocat (1970; Fig.), and Lavocat described lower teeth in detail (1976: 38–40), figuring three specimens (1976: Pl. 2, Figs. 5–7). All permanent teeth are tetralophate with the enamel extending farther rootward on the buccal side, especially on the hypoconid, than on the lingual side. They are to a considerable extent mirror images of the uppers (except that the latter have five crests), the anterior three lophids uniting at the protoconid, with the posterolophid initially set apart by confluence of the hypoflexid and metaflexid; these, however, become separated at an intermediate stage of wear (Fig. 23G). Hypolophid and metalophid are separated lingually by a rather deep mesoflexid, but metalophid and anterolophid are united lingually, even in unworn teeth (Fig. 24F,G), and there is thus an anterofossettid from the beginning of wear. The metalophid is a large crest that shows no signs of reduction. Lavocat (1976: 38) identified what we term the metalophid as "un mésolophide ou bras postérieur du protoconide," which, apparently, he considered to be the same thing. They are, of course, quite different. The mesolophid is a structure derived from the mesoconid, a cusp on the ectolophid behind the protoconid. The posterior arm of the protoconid has nothing to do with the ectolophid, and runs directly linguad from the posterior part of the protoconid. If it is large enough, and reaches the metaconid, it is known as the metalophid (or metalophulid II). The presence of both a mesolophid and a posterior arm of the protoconid is clearly shown in the Egyptian *Phiomys* (Wood, 1968: Fig. 1C; 1D, M_1; 1E; 1G, M_1). Nothing of this sort has been reported in any caviomorph.

There are two specimens of P_4 in the Princeton collections; Lavocat apparently had three. The posterior half of the premolar is identical to that of the molars

(Figs. 24E, 25A). There is apparently considerable variation in the anterior half of the tooth. Lavocat stated that one specimen, referred to by him (1976: 39) as SAL 103, with P_4 in process of eruption and M_1, shows essentially the same structure in the anterior half of P_4 as do the molars. However, his photograph of SAL 103 (1976: Pl. 2, Fig. 7) shows a jaw with M_{1-3} and the roots of dm_4. This photograph is apparently of the jaw that he identified as the one referred to the holotype (1976: 33), which he stated includes a left ramus with the alveolus of dm_4 and M_{1-3} (M_3 unerupted). This is also apparently the lower jaw mentioned by Hoffstetter and Lavocat (1970: 172) as having P_4–M_3 with a length of about 20.8 mm. It clearly is *not* the right P_4–M_1 they figured (1970: Fig., B.l.Dr.). The list of referred specimens given by Lavocat (1976: 33) does include one that agrees with the 1970 figure: "P4 inférieure en éruption et M1 SAL 106." This is presumably the specimen he identified (1976: 39) as SAL 103.

In both Princeton specimens of P_4 (Figs. 24E, 25A) there is a posterior extension from the anterolophid, suggesting the rear of an anteroconid, which dams or partly dams the anterofossettid. There are also one or more lingual cusps that close or nearly close the anterofossettid lingually. Lavocat's description of this area in SAL 108 (1976: 39; unfortunately the specimen was not illustrated) is rather hard to follow, but probably indicates a tooth essentially like the two figured here. The anterior half of P_4 of SAL 105 (Lavocat, 1976: Pl. 2, Fig. 6) is completely disintegrated, and shows nothing. It is possible that Lavocat's description of this specimen (1976: 39) was written before the anterior part of the tooth was destroyed. It is unfortunate that Lavocat published no stereophotos of the jaw with P_4 in process of eruption (SAL 106?), which he stated (1976: 39) is fundamentally like the molars in its pattern. This is in accord with the drawing published by Hoffstetter and Lavocat in 1970, but we wonder whether a ridge from the anterolophid might not be present deep within the anterofossettid, far enough below the surface in the partly erupted tooth so that its presence was not noted. If so, this would make it identical to the other premolars.

Dm^4 is somewhat broken and deeply worn in the type (Hoffstetter and Lavocat, 1970: Fig., B.l.; Lavocat, 1976: Pl. 2, Fig. 4). Fortunately, a specimen in the Princeton collection is only slightly worn (Fig. 24B). Lavocat (1976: 36) stated that the pattern was clearly the same as that of the molars, which is only partially correct. The two central lophs (protoloph and metaloph) are like those of the molars. The anteroloph seems to have had a large central anterocone, and there is a posteromesially directed hook from the buccal tip of the anteroloph, being the first stage in the development of an accessory crest. From the center of the posteroloph there arises a strong, forwardly directed crest, reaching as far anteriorly as does the hypocone. A similar forward extension of the buccal end of the posteroloph lies along the buccal margin of the tooth. If the anterior ends of these two crests should join, it would result in the formation of a neoloph; we suspect that this is exactly what happened in caviomorph evolution. Nothing remotely similar to all this has been reported in any tooth of any thryonomyoid. Replacement of dm^4 did not occur until after M^3 came into full usage.

There is a small root in front of dm^4 (Fig. 24B), either that of dm^3 or of P^3. The fact that the tooth was associated with dm^4 and was lost before the eruption of P^4 in all known specimens of *Branisamys* suggests that it was dm^3. However, the tooth produced a wear facet on the dorsal slope of the anteroloph of dm^4, lay dorsal to the overhang of the anteroloph, and could not have reached the level of the occlusal surface of the upper cheek teeth. In this position, it is difficult to see

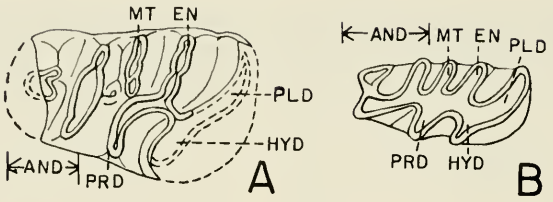

Figure 26. Tooth of *Villarroelomys bolivianus* Hartenberger compared with dm_4 of *Cephalomys arcidens*, ×5. A. GB no. 014 redrawn from Hartenberger, 1975: Fig. 2a, and restored according to our interpretation of its probable structure. B. Rdm_4 of *Cephalomys arcidens*, ACM no. 3013, redrawn and reversed from Wood and Patterson, 1959: Fig. 20A.

Abbreviations: AND—area derived from anteroconid; EN—entoconid; HYD—hypoconid; MT—metaconid; PLD—posterolophid; PRD—protoconid.

how this tooth could have erupted except after dm^4, which suggests that it might have been a P^3 that was shed along with dm^4 (Wood, 1969; 1970b: 245–246).

One badly broken dm_4 is present in the Princeton collection (PU no. 21987, Fig. 24G). This preserves no more than the posterior half of the pattern, which is the most molariform part of the caviomorph dm_4. In view of this, little more can be said of the specimen. Lavocat (1976: 39; Pl. 2, Fig. 5) described a similarly broken and more worn specimen in a ramus fragment that also includes M_1.

Lavocat (1976: 40–41) and Hoffstetter (1976: 10, n.) concluded that the type of *Villarroelomys bolivianus* (Hartenberger, 1975) was a dm_4, not an M_3, and suspected that it may have been a young individual of *Branisamys*, in which M_1 had not yet erupted. Lavocat further stated that Hartenberger was in essential agreement with him on this point (Lavocat, 1976: 40). We had independently arrived at the same conclusion. Certainly this tooth has nothing to do with the hydrochoerids. Because Lavocat felt that there was some possible uncertainty as to the reference to *Branisamys*, since the tooth of *Villarroelomys bolivianus* might represent an otherwise unknown genus closely related to *Branisamys*, he believed that the name *Villarroelomys* should be retained for the time being.

Hartenberger's illustration of the type of *Villarroelomys bolivianus* (1975: Fig. 2A) shows a tooth broken at both ends, with three crests reaching one margin, four the other, and with an assemblage of two or more cuspules near one end. The side view that he gave indicates, we believe, that the roots are somewhat divergent. This, together with the number and distribution of the crests, is convincing evidence that this tooth is Ldm_4 and not RM_3, as Hartenberger originally believed.

We have restored this tooth, from Hartenberger's illustration (Fig. 26A; our figure differs slightly, in the hypothetical portion, from the restoration given by Lavocat, 1976: Fig. 2J). There is sufficient resemblance to dm_4 of *Branisamys* (Fig. 24G) and to the corresponding tooth of *Cephalomys arcidens* (Fig. 26B) so that we feel considerable confidence in the general accuracy of the restoration. There are differences between GB no. 014 and Ldm_4 of *Cephalomys*. The Bolivian tooth is considerably larger and not quite so completely lophodont. Anterior to the metalophid, the anteroconid area of *Cephalomys* consists of an anterolingual cusp behind which there is a curved crest formed of an anterior buccal and a posterior lingual crest, whereas the anterior cusp of GB no. 014 is more isolated and is at least incipiently divided. On the other hand, the entoconid crest is shifted forward of the hypoconid-posterolophid crest as in dm_4 of *Cephalomys* (Fig. 26; Wood and Patterson, 1959: 340), and the

central crest, which we interpreted as the metalophid in *Cephalomys*, is also as in that genus.

On the basis of its size, general appearance, and agreement with what is preserved in undoubted dm_4 of *B. luribayensis*, we feel that GB no. 014 is dm_4 of this species. It certainly cannot be referred to *Sallamys* (Fig. 5D), *Incamys* (Fig. 19A,B) or *Cephalomys bolivianus*.

The upper incisor is a robust tooth that in its course describes a semicircle extending forward from its point of origin on the medial wall of the masseteric fossa above P^4. The posterior part of the tooth bulges into the infraorbital foramen, as in *Dinomys* (AMNH Mam. no. 46551). The anteroposterior diameter is greater than the transverse, the width/length ratio being between .67 and .75. Near the wear surface, the anterior face is flat over most of the width, becoming a little rounded laterally (Fig. 23A,B). Farther back, the anterior face is more rounded, and the pulp cavity becomes very large (Fig. 25B). The tooth is much more like that of *Dinomys* than like those of dasyproctids. The enamel extends for short, nearly equal distances onto the lateral and medial faces, again as in *Dinomys*. Near the wear surface (Fig. 23B), the pulp cavity is small, and shaped like a distorted figure 7 rather than like a distorted T as in *Dinomys*. The lower incisor was generally similar (Figs. 23E; 25D,E,G; Lavocat, 1976: 36; Fig. 3E,H). The enlargement of the pulp cavity beneath the rear of M_1 of PU no. 21987 (Fig. 25G) is related to the age of the individual (dm_4 still present) rather than to the position in the jaw, as is shown by adult specimens (PU nos. 22172 and 22173, Fig. 25H) that are broken farther to the rear.

Relationships. Hoffstetter and Lavocat compared *Branisamys* with *Neoreomys*, from which they distinguished it (1970: 172) "notammement par la brachyodontie, et par la réduction de M^3, ce dernier caractère excluant des liens directs." They were entirely correct in this, and they were fully justified in comparing *Branisamys* with *Neoreomys*, which, on the basis of the cheek teeth, it closely resembles. The two forms are definitely related, although not, we believe, at the family level. Lavocat (1976) made comparisons of *Branisamys* with other Deseadan rodents, with Oligocene and Miocene African rodents, but with no post-Deseadan South American genera except *Neoreomys*, and in this instance the comparisons were limited to the cheek teeth. He concluded (1976: 73) that *Branisamys* and *Incamys* should be placed in the same family and that *Branisamys* was clearly related to *Neoreomys*.

The discussion of the cranial characteristics given above and summarized in Table 7 indicates rather different relationships for *Branisamys* from those suggested by Hoffstetter and Lavocat (1970) and Lavocat (1976). Almost all available cranial characters point toward affinities with the Dinomyidae, and suggest relationships between *Neoreomys* and the Dasyproctidae as proposed by Wood and Patterson (1959: 324–328). It is interesting to note that, in early members of these two families at least, the cranial characters give a better insight into familial relationships than do those of the cheek teeth. Table 7 demonstrates that, insofar as the characters available for *Branisamys* are concerned, ?*Simplimus* is somewhat aberrant with respect to known dinomyids, sharing more features with dasyproctids than with *Dinomys*. We give more weight to those in common with the latter, however, and follow Fields in his familial assignment. The family having been in existence since at least the beginning of the Oligocene, an early radiation within it may have taken place, giving rise to the Friasian *Simplimus*, a side line independent of the later dinomyid radiation.

Derivation of the cheek teeth of later dinomyids from those of *Branisamys*, or some similar form, would not present serious difficulties. The requirements for

TABLE 7. COMPARISONS OF *Branisamys* WITH DINOMYIDS AND DASYPROCTIDS.

	Simplimus?							
	schurmanni	*angustus*	*Drytomomys*	*Dinomys*	*Branisamys*	*Neoreomys*	*Incamys*	*Dasyprocta & Myoprocta*
Anterior face of upper incisor	nearly flat	rounded	—	flat	nearly flat	nearly flat	rounded	rounded
Enamel equally far on lateral and medial faces of I^1	no	—	—	yes	yes	yes	no	no
Rostrum	long, stout	long, slender	short, stout	short, stout	short, stout	short, slender	short, slender	very long, slender
Rostrum sloping upwards on ventral surface	no	—	—	yes	yes	yes	no	no
Fossa for masseter on rostrum very long	shorter	—	—	yes	yes	shorter	shorter	shorter
Nasals widest point	anterior	—	—	middle	middle	anterior	nearly parallel-sided	nearly parallel-sided
Fronto-maxillary suture transverse across skull	no	—	—	yes	no	yes	no	no
Orbital portion of frontal flat	rounder	—	—	yes	yes	rounder	rounder	rounder
Vertical plate of lacrimal	absent	—	—	absent	absent	present	probably present	present
Premaxillary-maxillary suture turns back behind incisive foramen	yes	straight across	straight across	yes	yes	straight across	straight across	straight across
Cheek-tooth rows converge anteriorly	very little	no	yes	yes	somewhat	yes	yes	no
Fossa for *M. buccinator*	shallow	deep	deep	shallow	shallow	deep	deep	deep
Opening into lacrimal canal through side of maxillary	no	—	—	small	perhaps; if so, small	very large	probably; if so, large	very large
Groove in bottom of infraorbital foramen for nerve and blood vessels	yes	—	yes	yes	yes	no	no	no
Incisor base	in front of P^4	—	above P^4	above front of M^1	above P^4	in front of P^4	in front of P^4	in front of P^4

this would be progressive elongation of the teeth, already foreshadowed in unworn teeth of *Branisamys*, further separation of the lophs and lophids, together with ever-increasing height of crown, culminating in the hypselodonty of the late Tertiary and Quaternary forms. The anteroloph and posteroloph are already, in *Branisamys*, well on the way to independent status, and the changes required to isolate the protoloph as the second of the dinomyid upper cheek-tooth crests would not seem to have been very profound. Due to the absence of dinomyids from the Colhuehuapian and Santacruzian of Patagonia, the details of the process remain obscure. When the dinomyid record begins again, we see in *Drytomomys*, from the La Venta local fauna of Colombia, of Friasian age, an early member of the spectacular later Tertiary dinomyid radiation.

Fields (1957: 323) referred his material of this form, correctly we believe, to Anthony's *Drytomomys aequatorialis*, but he synonymized *Drytomomys* with *Olenopsis*. As we have previously indicated (Wood and Patterson, 1959: 361, n. 21), the syntype material of Ameghino's type species, the Santacruzian *O. uncinus* (1889: 145), is partly lost, partly referable to *Neoreomys*, and partly clearly different from Fields' material. Until such time as additional specimens are found in the Santa Cruz, clearly determinable as *O. uncinus* and clearly diagnostic, we believe that the reference of other species to this genus will serve no useful purpose. We therefore retain Anthony's generic name, *Drytomomys*, for *aequatorialis*. The Pliocene *Olenopsis typicus* Scalabrini (Ameghino, 1889: 901) is not congeneric either with *O. uncinus* or with *D. aequatorialis*, and was made the type of *Paranamys* by Kraglievich (1934: 73).

The type of *D. aequatorialis* was found in Ecuador, apparently on the floor of a cave in tuffaceous rock (Anthony, 1922). On the basis of these scanty data it could have been contemporaneous either with the tuff or with the cave. Anthony decided in favor of the latter possibility, and considered the species to be Pleistocene in age. Fields (1957: 324, n. 5) discounted this. Hoffstetter (1952: 124–125) has reported that on geological grounds the tuff may be of late Tertiary age. It would therefore appear probable that the specimen had weathered out of the roof or walls of the cave, and that the deposit from which it came is approximately contemporaneous with part of the Honda Formation of Colombia.

In *Drytomomys*, there was a highly progressive development of subparallel diagonal crests in the upper molars, fully separate initially but rapidly uniting with wear along the buccal sides of the teeth. The crests of the premolar seem to have been even more independent than those of the molars. This separation of the lophs is associated with a very considerable degree of hypsodonty. The posterolophid of the lower molars of *Branisamys* is already well on the way toward separation, with the three anterior lophs joined buccally, and the two anterior united lingually as well. *Drytomomys aequatorialis* shows the same features (Fields, 1957: Fig. 16a), but again with somewhat longer independence of crests and much greater hypsodonty than in *Branisamys*. The various later dinomyids could have been derived, with relatively little difficulty, from something very similar to *Branisamys*, by way of something like *D. aequatorialis*.

For these reasons, we have no hesitation in referring *Branisamys* to the Dinomyidae (since this was written, Hartenberger, 1975, has included the genus, with a query, in this family).

The less pronounced, but still very real resemblances of *Branisamys* to the Dasyproctidae we interpret as indicating that the two families were closely related in Deseadan time. We formerly (1959: Fig. 34) showed the Superfamily Chinchilloidea as extending back to the Deseadan

with two families, the Chinchillidae and Dasyproctidae, and the Heptaxodontidae, Cuniculidae and Dinomyidae as arising from the Dasyproctidae at some unknown (but perhaps mid-Tertiary) time. This must now be modified since the Dinomyidae, in the form of *Branisamys*, were already present in the Deseadan, although not far removed from a common ancestry with the Dasyproctidae. We now agree with a growing consensus that dinomyids, dasyproctids and cuniculids should be removed from the Chinchilloidea and returned to the Cavioidea. The broader affinities of all groups are discussed below and the implications for caviomorph higher taxonomy of recent comparative anatomical and karyological work are considered (pp. 509–512).

Kraglievich (1926, 1930a, 1931, 1932a) proposed no less than four families, one of them including four subfamilies, for the reception of the genera involved in the later Tertiary radiation of what we consider to have been dinomyids. Simpson (1945: 95–96), who placed these later Tertiary genera in the Heptaxodontidae, reduced Kraglievich's swollen array to three subfamilies. ?*Simplimus* is a member of Kraglievich's Potamarchinae in this scheme, and *Drytomomys* would fit without strain into his Eumegamyinae (=Dinomyinae), but *Branisamys* could not, without knowledge of intermediate stages, be fitted into any subfamily. In view of the enlarged dinomyid vistas now opened up, it would be the part of wisdom to hold subfamilial divisions in abeyance for the time being.

Caviomorpha *inc. sed.*
Luribayomys Lavocat 1976
Luribayomys masticator Lavocat 1976

Luribayomys masticator Lavocat, 1976: 64–68; Fig. 3D; Pl. 5, Figs. 1–3.

This taxon is based on a rostrum with the incisors broken off at the alveoli and with the roots of both premolars and, in part, of LM^1. For all other Deseadan rodents (except *Palmiramys*—see below, p. 449) we have some knowledge, often good, of the cheek teeth, and the taxonomy is to a large extent based upon them. *Luribayomys* stands outside this circle. It is about the size of *Sallamys*, from which it differs in incisor cross section and in the possession of a much wider rostrum. Its rostral structure would appear to separate it from the other forms—*Platypittamys*, *Incamys*, *Cephalomys*, *Branisamys*—in which this part of the anatomy is known. It is much too small to belong to either *Protosteiromys medianus* or *P. asmodeophilus*. The rooted cheek teeth exclude it from *Scotamys*. This still leaves a number of forms with which it cannot at present be compared: *Migraveramus*, *Deseadomys*, *Xylechimys*, *Litodontomys*, Dasyproctidae aff. *Neoreomys*, *Asteromys* and *Chubutomys*, aside from the possibility of its being a valid genus. It cannot even be placed as to family. For the present it must be left indeterminate, as a clear case of a *nomen vanum* (Simpson, 1945: 27).

We can only join Lavocat in the hope for a fortunate find that will include both rostrum and cheek teeth and thus permit characterization of this genus.

Palmiramys Kraglievich 1932b (by A.E.W.)
Palmiramys waltheri Kraglievich 1932b

Kraglievich (1932b: 314–316) described *Palmiramys waltheri* as a new genus and species, based on a lower jaw from the Fray Bentos Formation of Uruguay. He referred it to the Acaremyinae, then included in the Erethizontidae, but gave no figures, and his description was not very illuminating.

Mones and Ubilla (1978: 154) concluded that the Fray Bentos was Deseadan because it contained *Propachyrucos* and *Proborhyaena*, both characteristic Deseadan genera.

Mones and Castiglioni report the discovery of a drawing (1979: 78, Fig. 1),

presumably of the type specimen which they state may be presumed to have been lost. This drawing accompanied the manuscript of Kraglievich's paper. Mones and Castiglioni conclude that *Palmiramys* was probably a dasyproctid.

The measurements that Kraglievich (1932b: 315) gave for the type of *Palmiramys waltheri* are very close to those of *Migraveramus beatus* (Table 1; Fig. 3). His original identification of *Palmiramys* as an acaremyine would also be in accord with its being close to *Migraveramus*. It would be difficult to visualize, however, how wear of Deseadan octodontid teeth could produce a pattern such as that figured by Mones and Castiglioni (1979: Fig. 1).

A comparison of this figure with all available illustrations of Deseadan rodents indicates that the only closely similar form is *Incamys* (cf. Figs. 16, 19 and Mones and Castiglioni, 1979: Fig. 1). Mones and Castiglioni made no specific comparisons of *Palmiramys* with *Incamys* or any other rodents. Kraglievich's original description could fit *Incamys*, but it could equally well refer to some other genus. His measurements (1932b: 315) are those of an animal half to two-thirds the size of *Incamys bolivianus*.

Palmiramys waltheri appears to have all the characteristics of a *nomen vanum*.

DISCUSSION

Conflicting Theories of the Origin of the Caviomorpha

Description and taxonomic assessment of the Bolivian Oligocene rodents having been completed, we now turn to the broader questions that involve them, their ancestors and descendants, and their relatives in other parts of the world.

There are at present two, in large part conflicting, principal hypotheses concerning the origin, interrelationships and dispersal of hystricognathous rodents. As background for what follows, these opposing concepts must again be compared.

One of them, revived in modern form by Lavocat (1969) and by Hoffstetter and Lavocat (1970), and subsequently developed by both authors severally (Hoffstetter, 1971; 1972; 1975; Lavocat, 1971a; 1973: 254–258; 1974a; 1974b; 1976: 74–84; 1981), holds that the Suborder Hystricognathi arose in Africa from waif immigrant European paramyids, possibly related to the European Theridomyidae, that had arrived in Africa in late Paleocene or earliest Eocene time (well before the evolutionary origin of the Theridomyidae). These ancestors then gave rise to the Thryonomyoidea, from which evolved, in Africa, the Bathyergoidea and, possibly, the Hystricidae (alternatively, these last arose from thryonomyoids supposed to have reached southern Asia from Africa, as waif immigrants, around the middle Eocene). The New World Infraorder Caviomorpha descended from African thryonomyoids that had been rafted, perhaps twice (if the Erethizontoidea are as distinct as Bugge has suggested), in middle Eocene time, across a then-narrower South Atlantic Ocean. The proponents of this view tend either to dismiss the awkward fact that subhystricognathous and hystricognathous Eocene rodents are known only from North (including Middle) America as an irrelevancy, or to neglect these rodents entirely. Hussain *et al.* have recently proposed an extreme version of this hypothesis (see below, pp. 504, 515).

The second hypothesis was sketched by us in 1970 and further developed by Wood (1972, 1973, 1974b, 1975a, 1977b, 1980b, 1981); we here carry it further. It holds that the Hystricognathi arose in the late Paleocene of North America as franimorph reithroparamyids. A group, or groups, of these crossed to Asia, via Beringia, early in Eocene time, and there gave rise, directly or indirectly, to the Thryonomyoidea and Hystricoidea. Another franimorph group, the cylindrodonts, reached Asia in the late Eocene, giving rise to the Tsaganomyidae in Asia

and, later, to the Bathyergidae in Africa. The thryonomyoids reached Africa, as waif immigrants, from southwestern Asia during the late Eocene; the bathyergoids and hystricoids, as dry land immigrants, during pre-Burdigalian and late Miocene times, respectively. The ancestors of the Caviomorpha reached South America, as waif immigrants, from southern North America (i.e., Middle America) in middle Eocene time. McKenna (1981: 63) has proposed a possible variant in the method by which the caviomorphs reached South America from the north. The proponents of this view of things consider the North American Eocene subhystricognathous and hystricognathous rodents as very relevant indeed.

Earlier, at a time when nothing was known of North American Eocene hystricognaths and next to nothing of the paleontology of the Old World ones, we (Wood and Patterson, 1959: 419) concluded "that the Hystricomorpha and Caviomorpha have derived those characters, which they hold in common, independently and subsequent to their geographic separation." The presumed ancestors would have been relatively undifferentiated paramyids. We added: "This is extreme parallelism," which is true, but not much, if any, more than has been reported on numerous occasions among the rodents (Engesser, 1979: 41–42; Lavocat, 1951; 1954: 127; 1955: 634; Vianey-Liaud, 1972; Wood, 1935: 249; 1936b; 1947: 156–161; 1950: 90–97; 1965: 122–124; 1974b: 38–41; 1975a: 76–77; 1977a: 133–136; 1981: 82; in press a; Wood and Patterson, 1970: 631). We do not know how many of the morphological characteristics of modern hystricognaths (Wood, 1975a: Fig. 1) had been acquired by the Eocene franimorphs; certainly at least hystricognathy and hystricomorphy had been. And certainly all features that characterize modern hystricognaths did not appear simultaneously, fully developed (Wood, 1980c: 270), but must have evolved gradually and, almost certainly, independently and at different times. Dawson (1977: 197, n.) commented that the hystricognathy of the Reithroparamyidae was "'incipient' only *a posteriori*." However, as pointed out elsewhere (Wood, 1980c: 270), unless hystricognathy arose as a single genetic mutation of one sort or another, it must have been a gradual development, its initial stages barely detectable. Since hystricognathy was the first (and only universal) hystricognath character to evolve, the initial changes were presumably the result of selective pressure for lengthening the *M. pterygoideus internus*, as an adaptation to increase gnawing ability. This was followed relatively soon (but with a definite time lag) in many groups by the evolution of hystricomorphy, resulting from a similar lengthening of *M. masseter medialis*, presumably as an analogous adaptation. This same change also occurred independently in several sciurognath lines.

In this theory, the resemblances between the Old and New World hystricognaths (and, very probably, among the Thryonomyoidea, Bathyergoidea and Hystricidae) other than hystricognathy (and possibly the correlated deepening of the pterygoid fossa) and, perhaps, hystricomorphy, have all resulted from parallel evolution during the 50-odd million years since the ancestors of the Old and New World hystricognaths separated in the early Eocene.

The two hypotheses are not mutually exclusive in their entirety. They are in agreement that, so far as our present knowledge goes, all *living* hystricognathous rodents form a natural suborder, the Hystricognathi; that Old and New World hystricognaths are distinct, infraordinally; and that the thryonomyoids and caviomorphs reached Africa and South America as waif immigrants, the latter around the middle of the Eocene. Under either view, hystricognath evolution in the Old and New Worlds has gone on independently for over 40 million years.

Beyond the points just indicated, the common ground between the two viewpoints ends and disagreements begin. Discussion of the evidence bearing on these disagreements, as presented below, must range widely, from paleogeography to parasitic nematodes, from comparisons of faunas to the excruciating minutiae of molar tooth morphology. As a beginning, we will now attempt to set the stage.

First, however, perhaps a third hypothesis, that of Croizat, should be mentioned for the sake of completeness. As recently stated by him, he feels it to be a fact that the ancestors of the Hystricomorpha "negotiated [the South Atlantic] in the Cretaceous or even earlier" and, further, "At some unspecified time earlier than the beginning of the Tertiary, certain very primitive 'proto-rodents' originated in a then unitarian continent of Gondwana. When this continent split into a later South America and Africa, respectively, these 'proto-rodents,' already on the way to evolving as taxonomically definable 'hystricomorph rodents,' turned 'American' and 'African' by right of the new continental geography . . ." (1979: 251). As pointed out by Wood (1980a), the documentary evidence for this hypothesis is nonexistent.

And, finally, as some authors have pointed out, since there is evidence supporting both the African and the Middle American origin of the Caviomorpha, there is justification for adopting a noncommittal position (Simpson, 1980: 140–141; Hartenberger, 1980: 296).

Eocene Geography

According to plate tectonic reconstructions, the world in Eocene time was well on the way toward conditions now existing. The present configuration of the continents was at least foreshadowed, although the relations of land and sea and the spacing of the continents relative to each other and their interconnections, or lack of them, were in many cases significantly different (Fig. 27). South America and Africa (*cum* Arabia), which had begun to separate at about 125 m.y.b.p., were, by mid-Eocene time, separated by a South Atlantic Ocean that was some 1300 km wide at its narrowest point. Africa was isolated from Europe and Asia, and South America from North America. Middle America, the tropical portion of the continent, seems to have ended in what is now Honduras and Nicaragua. North America had a land connection with Europe at the beginning of the Eocene, which was quickly broken (Wood, 1977b: 100), and another, also of no great duration, with Asia via Beringia at the same time; the latter was re-established for a while in the latest Eocene or the early Oligocene. Europe and Asia were separated by a seaway that lasted throughout the Eocene. This was the "Uralian trough" of Patterson (1954: 192), the Turgai Strait of Thenius (1959: 107; McKenna, 1975b: Fig. 1). One result of its elimination was the "grand coupure," the long-recognized major change in Europe between the mammalian faunas of the early and middle Oligocene (Stehlin, 1909: 502–508). India and southeastern Asia were in their present positions by the middle Eocene. The whereabouts of Australia, New Guinea, and New Zealand during the Eocene are less certain—but in any event irrelevant to the present study; rodents did not reach Australia until the early Pliocene (Archer and Bartholomai, 1978: 15; Wood, in press b).

The evidence provided by Eocene mammalian faunas, so far as these are known, is in accord with such continental relationships. South America and Africa (to judge from the absence of similarities between the Eocene faunas of South America and the Fayum fauna of Africa) had long been isolated. The faunas of northern North America and Europe were closer in early Eocene time than they were ever to be again. The faunas of

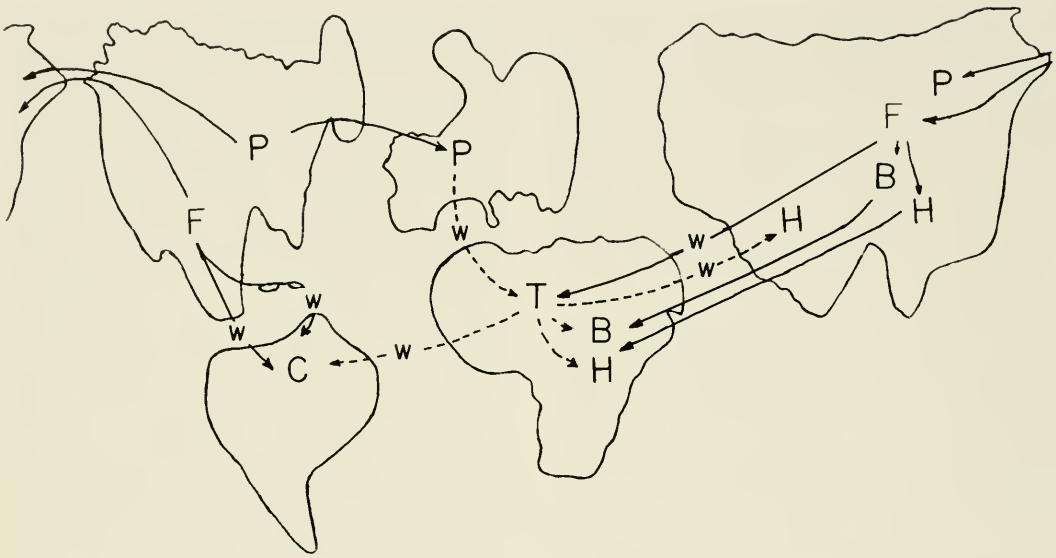

Figure 27. The world in Eocene time showing the distribution of the hystricognath groups and the Paramyidae, and the evolutionary relationships of hystricognath groups according to Lavocat (dashed lines) and according to us (solid lines). B—Bathyergoidea; C—Caviomorpha; F—Franimorpha; H—Hystricidae; P—Paramyidae; T—Thryonomyoidea; *w*—waif transport. Intercontinental migrations not marked *w* are assumed to have been via dry land. In our view bathyergids and hystricids reached Africa in early and late Miocene time, respectively.

Europe and Asia were sufficiently distinct to show that the Turgai Strait was a real barrier to interchange, whereas there were many similarities between the faunas of North America and northern Asia (Dawson, 1977).

Discoveries in the early Eocene of China of such typically Wasatchian mammals as *Homogalax* and *Heptodon*, unknown in Europe (Chow and Li, 1965), and of a paramyid in the size range of small species of *Microparamys* (Li *et al.*, 1979) strongly indicate that a connection between Asia and North America was in existence at that time. Confirmatory evidence is provided by recent finds of mammals referable to or allied with North American genera in the early Eocene Naran Bulak Formation, Mongolian People's Republic (Dashzeveg and McKenna, 1977, and references there cited). These authors point out that the presence in the Naran Bulak of *Altonius*, an omomyid of North American anaptomorphine affinities, indicates a climate in the Bering Strait region sufficiently clement to support very small primates. The Eocene, especially its earlier stages, does seem to have been a rather warm epoch.

As an aside (by B.P.), categorical statements that marsupials were absent in Asia may prove to have been premature. Didelphids reached Europe, via the North Atlantic early Eocene connection, and they could have reached Asia, via Beringia, at about the same time. Further, it is also conceivable that in late Cretaceous time they could have inhabited the river valleys of eastern Asia where they would have encountered environments similar to those of the western interior of North America, surroundings more congenial to them than the drier, more upland conditions that seem to have prevailed in Central Asia at that time.

Until very recently, all Eocene terrestrial mammals recorded from India and

Pakistan were of Holarctic affinities. There was no trace of any peculiar endemic mammals such as one might expect to have evolved on the subcontinent during its long isolation and postulated northward passage. The large mammals from the middle Eocene of Pakistan, recently described by West (1980) include a variety of cetaceans, as well as a considerable number of land mammals. These are all, with one exception, referable to Holarctic families, although generally to endemic genera. The one exception is the genus *Anthracobune*, identified by West as a primitive moeritherе, which he considered (1980: 530–531) might indicate a south Asian origin of this group. Sahni and Mishra (1975) have also reported a probable moeritherе from the middle Eocene of India. No other possible descendants of the presumed south Asian Mesozoic or Paleocene mammals have been reported.

Whatever its position may have been in the Permian, the Indian subcontinent could not possibly have docked at its present position bearing a mammalian cargo of the kind revealed by its known Eocene fossils. The striking lack of endemism in the Indian-Pakistani biota as a whole is, in fact, rather difficult to reconcile with plate tectonic theory. It has been seriously suggested that the (presumed) endemic biota was essentially wiped out as a result of climatic stresses encountered during the northward passage. This strikes us as fatuous: life is more adaptable than that, and continents do not move that rapidly.

The presence of what may be primitive moeritheres in the Eocene of Pakistan and India is the only suggestion of terrestrial mammals that show any affinity to those that evolved on Africa while that continent was isolated, and it is possible that they were the ancestors of the late Eocene and Oligocene African moeritheres. The absence of other mammals of African aspect would seem to refute the idea expressed by Hoffstetter (1975: 524) that, in the Eocene, the Pakistan-Indian area was part of the African-Arabian block, and carried African hystricids to Asia. This idea perhaps was based on the then unstudied Eocene rodents of Pakistan (Hussain *et al.*, 1978). However, as indicated below (p. 504), these rodents were apparently all sciurognaths and had nothing to do with the ancestry of either the Thryonomyoidea or the Hystricidae.

Distribution of Hystricognathous Rodents in the Eocene

The Order Rodentia was certainly of northern origin. Members of it first appear in the latest Paleocene of western North America. These forms, which had already acquired all the basic ordinal characters, are referable to two very closely related families, the sciurognathous Paramyidae and the incipiently hystricognathous Reithroparamyidae, the latter, in our opinion, the ancestral stock of all later members of the Hystricognathi.

Where, in the northern hemisphere, the order arose is still uncertain. Europe would appear to have been a most unlikely place. No reithroparamyids are known from there, although Michaux (1964) referred two species to *Reithroparamys*; he later (1968: 155) made one of them the type species of *Meldimys*, a member of the sciurognathous Ailuravinae, and stated (1968: 173–174) that the other was indeterminate as to genus; both were reported only from isolated teeth, so that there was no information as to their possible hystricognathy. The paramyids that arrived in Europe at the beginning of the Eocene gave rise to a rodent fauna that evolved in isolation throughout the epoch, with a considerable variety of strictly endemic forms.

This leaves us with North America, where the early Eocene record is fairly good, or Asia, where it is not. The only early Eocene Asian rodent, so far as we are aware, is that described as *Micropar-*

amys lingchaensis from Hunan (Li *et al.*, 1979: 76), which is, we believe, a new genus and not *Microparamys*. Dr. Li informed one of us (A.E.W., April 1981) that he had reached the same conclusion and that a new name and a re-assessment of the relationships of this form are in preparation. In Figure 27 we tentatively suggest a North American origin for the rodents, but stress that an Asian one would have just about as much evidence in its favor (Hartenberger, 1980: 300). However, we believe that such an origin would not affect our thesis appreciably.

The group that, in our opinion, is the most probable ancestral stock for the rodents, the primitive primates (Wood, 1962a: 253–254), is better known in North America than in Asia. The Asiatic Eurymylidae, sometimes cited as having rodent affinities, were close to the ancestry of the lagomorphs (Wood, 1942; 1957: 417–418), but, so far as they are known at the present time, do not seem to A.E.W. to have had any special relationship to the rodents. Li (1977: 116–117) described *Heomys orientalis*, the most rodent-like eurymylid so far reported. Gingerich and Gunnell (1979: 151) cited this form as "appearing closely related to rodent origins." However, a cast of the type specimen, sent to one of us (A.E.W.) by Dr. Li, shows that the molars, particularly M^{1-2}, have a well-developed hypocone, extending linguad of the protocone, much more prominent and quite different in appearance from anything seen in primitive rodents. Whereas the hypocone of the rodents arises from the area where the posterior cingulum joins the protocone, that of *Heomys* seems to have grown from a posterior cingulum not connected with the protocone. Furthermore, the paracone is isolated from the protocone, lying behind the protoloph which is formed by the protocone, protoconule and anterior cingulum, a condition unknown among the rodents, but suggestive of the situation in early lagomorphs (Wood, 1940: Fig. 114). There apparently were a number of late Paleocene groups independently evolving gnawing incisors, at least sometimes in different geographic areas. With the evolution of the rodents, these competing lines were quickly replaced except, apparently, in restricted environments. One line, the lagomorphs, later acquired the capability of competing successfully with the rodents.

Reports of teeth identified as *Franimys*? by Sahni and Srivastava (1976: 923–924) from the middle Eocene of India, and of phiomyids or of "une famille protophiomyidée" by Lavocat (1973: 165–166) from the middle Eocene of Pakistan, are readily interpretable in terms of our view that hystricognaths were present in the Eocene of Asia—presumably these teeth had been housed in hystricognathous or subhystricognathous jaws. However, it is also possible that all of these teeth are referable to the Family Chapattimyidae of Hussain *et al.* (1978), which were members of the sciurognathous ctenodactyloids. Since the above was written, Hartenberger (1980: 288) has adopted this last point of view. Sahni (1980: 26) accepted the ctenodactyloid relationships of these forms, but considered *Chapattimys* to be a synonym of *Metkamys* Sahni and Srivastava (1976).

There obviously was extensive rodent evolution going on in Asia during the Eocene, even though we are still only barely aware of much of it. The large series of rodents described by Shevyreva (1976) is a beginning of a demonstration of this activity. The rodents that she identified as sciuravids (1968, 1971a, 1971b, 1972a, 1972b, 1972c, 1976), following Dawson's (1964: 11) tentative reference of *Advenimus* to the Sciuravidae rather than to the Ctenodactylidae, but all since transferred to the Ctenodactylidae by Wood (1977a), illustrate once more the development of hystricomorphy among sciurognaths as an occurrence independent of what happened among the hystricognaths. Quite a variety of paramyids

has been reported from the Asian Eocene (Chow *et al.*, 1973: 179; Li, 1975; Li *et al.*, 1979: 79), although Hartenberger (1980: 288) considered *Yuomys* and *Microparamys lingchaensis* to be ctenodactylids. Even if Hartenberger is correct, and both of these forms are ctenodactylids, they do not seem to me (A.E.W.) to be anywhere near as distinct from paramyids as he indicated (1980: Fig. 2).

Cylindrodonts—*Ardynomys* and *Pseudocylindrodon*—had reached Asia by the late Eocene and middle Oligocene, respectively (Vinogradov and Gambarian, 1952: 14–15; Kowalski, 1974: 155–156; Shevyreva, 1976: 41–46, Fig. 16). As pointed out elsewhere (Wood, 1980b: 6; 1981: 85–87; in press a: Fig. 1), the cylindrodonts were incipiently hystricognathous (subhystricognathous). The presence of the specialized, fully hystricognathous *Tsaganomys* and its relatives in the middle Oligocene of Central Asia (Shevyreva, 1976: Fig. 16), which we recognize as a family of the Bathyergoidea (see below, pp. 515–516), and which are believed by at least one of us (A.E.W.) to have been derivatives of the subhystricognathous cylindrodonts, is an indication that much more was going on in this area.

Thryonomyoids reached Africa as waif immigrants late in the Eocene (Wood, in press b), and, we believe, unquestionably from southwestern Asia. They first appear in the record in the early Oligocene Jebel el Qatrani Formation, where they are rare faunal elements (Table 11) that had just begun their radiation. Savage (1969: 69; 1971: 220) reported rodents as being present in the late Eocene of Libya. Later he concluded (Wood, 1974b: 33) that these deposits were early Oligocene, contemporaneous with the lower level of the Jebel el Qatrani Formation of Egypt. There is no certain evidence that any non-thryonomyoid rodents were present in Africa before early Miocene time (see below, p. 467).

The caviomorphs reached South America, also as waif immigrants, in the middle Eocene (Wood, in press b). They first appear in the record in the early Oligocene Deseadan, by which time they were numerous and diversified. Had it not been for these successful landfalls on the South American and African continents, the Hystricognathi would probably now be limited to the bathyergids and hystricids, there would be no lively, widely ranging hystricognath controversy, and life on the rodent front would be duller.

Lavocat (1976: 80) believed that Eocene ocean currents would have facilitated transport of rodents on natural rafts from Africa to South America across an ocean at least 1500 km wide. He stated (1976: 61) that "diverses observations de navigateurs ne permettent pas de considérer comme infranchissable à des radeaux naturels" such a distance. Unfortunately, he gave no documentation for such "diverses observations" (Wood, 1977b: 104, n.). More recently, he has gone even farther, stating "mariners are said to have found living rodents on trees rafted as far as 2,000 km from the shores (Chaline, pers. comm.)" (Lavocat, 1978: 86). This is still anecdotal evidence, and not documentation. He and Hoffstetter (1975: 526) also believed that currents sweeping westward through the gap between North and South America would have been strong enough to have prevented rafting from the former to the latter. We know of no evidence as to the velocity of such supposed currents (see also Simpson, 1978: 326). There should, logically, be similar currents now sweeping westward between Australia and New Guinea, which do not seem to have prevented the eastward spread of Asiatic mammals, especially the Muridae, through the East Indies to New Guinea and thence to Australia.

Moreover, Lavocat's beliefs are based on the assumption that all was quiet around the Caribbean at the time, which was far from the case. Reporting on the geology of northwestern Colombia, Haf-

fer, whose opinions carry weight due to his years of work there as a petroleum geologist, found (1970: 615–618, Fig. 6) clear evidence of two Tertiary episodes of orogenic uplift, each followed by subsidence, prior to the late Pliocene elevation of the Isthmus of Panama. It should be noted that Haffer's work was carried out in complete independence of any consideration of the South American Tertiary mammalian record, to which he did not refer. The first orogenic uplift occurred toward the end of the middle Eocene, the second toward the end of the middle Miocene. We regard it as no mere coincidence that these uplifts coincide with the presumed times of arrival of, first, rodents and primates in South America and, second, of ground sloths in North America and an extinct group of procyonids in South America.

To digress for a moment, infatuation with Africa as a source for South American Tertiary mammals has not yet embraced these raccoons, perhaps because no member of the family has ever been recorded from Africa. It has, however, extended to the hesperomyine cricetids, whose fossil record in South America dates from the end of the Pliocene. Hershkovitz (1972: 325) has suggested that the ancestors of these rodents may have been rafted across the Atlantic from Africa in the early Teriary. Satisfactory evidence of the presence of hesperomyines in North America since the late Miocene (Baskin, 1978: 131–134) disposes of this possibility, which in any event ran directly counter to the complete absence of possible hesperomyine ancestors in Africa or of any non-caviomorph rodents in the South American record prior to latest Tertiary time.

The orogenic episodes reported by Haffer are by no means all that was happening in this area. During later Cretaceous time the Caribbean-East Pacific Plate with its island arc advance guard was moving eastward between Central and South America (Malfait and Dinkelman, 1972). A partial connection through such an island arc is what would be required to account for the presence during the early Tertiary of, e.g., notoungulates in both Americas and of condylarths in South America, which last, had they been found in the north, would without hesitation have been placed in Holarctic families. Malfait and Dinkelman further concluded that, prior to the early Oligocene, the Caribbean Plate had decoupled from the East Pacific one, and that the Middle America Trench had extended south-southeastward and had become bordered along its northern flank by a chain of volcanic islands. These, following a period of quiescence, had combined by middle Miocene time to form the western portion of the present Isthmus of Panama. That these plate events bore some relation to the episodes of orogenic uplift and of subsidence reported by Haffer (whose work was evidently unknown to Malfait and Dinkelman) in extreme northwestern South America is a reasonable assumption. In other words, waif transport between the Americas would have been possible at the times that the fossil record indicates that it occurred. Ladd's views (1976) on the relation between the Americas and the Caribbean Plate do not contradict this possibility.

More recent work seems to give even stronger support to the probability that there was a Central American-Antillean land area that could well have been involved in the caviomorph migration to South America. Perfit and Heezen (1978) indicate that there was extensive uplift of Middle America from southern Mexico to include Nicaragua, as well as of the Cayman Ridge and the Nicaraguan Plateau now beneath the western Caribbean. As a result, there was deposition of a thick series of continental sediments all through this area and the Greater Antilles during the latter part of the Eocene (*op. cit.*: 1155, abstract; 1169). "Each clastic rock type appears to have a red-bed equivalent suggestive of subaerial and/or deltaic

depositional environments .... The presence of plutonic clasts suggests a great deal of erosion and uplift in order to expose the [Cretaceous] intrusives by the Eocene" (*op. cit.*: 1169). Their Figure 10 indicates that there was a pre-Oligocene Cayman Ridge and Nicaraguan Plateau land mass that was continuous or nearly so from Nicaragua through Jamaica, Oriente Province of Cuba and Hispaniola. Here the rodents would have made enough easting so that they could have achieved a landfall in northern South America by island-hopping through the Lesser Antilles (either the present islands or their Eocene predecessors as suggested by Malfait and Dinkelman, 1972), crossing Lavocat's hypothetical east-to-west current from northeast to southwest (Wood, 1977b: 104; 1981: 87–88).

There seems to be a vague impression afloat that plate tectonic theory is somehow more favorable toward latest Cretaceous and earlier Cenozoic raft transport from Africa to South America than toward such transport between the Americas. If anything, as indicated above, the evidence shows that it was the other way around. Webb (1978: 395) reached conclusions similar to ours as to the distances separating South America from Africa and North (or Middle) America during the Oligocene.

If the caviomorphs, or their immediate ancestors, reached South America from the north, the place of departure of the waif emigrants was southern, or tropical, North America. Southward from the border between the United States and Mexico this portion of the continent is practically a *terra incognita* as regards its earlier Tertiary mammalian faunas. It is a large region, whose size is perhaps not always appreciated. At the beginning of the Cenozoic, its area was about half that of present-day Europe west of the USSR, and it spanned some 20° of latitude, a distance approximately equal to that between the Straits of Gibraltar and northern Scotland (Wood, 1981: 87). This area is all part of the region defined as, biogeographically, Middle America by Ferrusquía (1978: 198). Middle America "must long have been a center of adaptation and local radiation of faunal elements specifically adapted to its special conditions . . ." (Simpson, 1950: 389).

Reviewing the Recent mammalian fauna and what evidence of past ones was then available, Patterson and Pascual (1972: 255–257, Table 3) concluded that "the North American tropical peninsula was evidently a fact of ancient geography, and there is convincing Recent and suggestive Tertiary evidence that its mammals are and were distinctive to some degree within the continental fauna as a whole." Such suggestive evidence is increasing. Jacobs (1977: 518) and Baskin (1978: 133) see indications of southern elements within late Miocene rodent faunas in Arizona. Wood (1973: 32; 1974a: 102–104; 1975a: 78; 1981: 87) has concluded that rodent faunules from the middle Eocene to the early Oligocene of southwestern Texas and from the middle to late Eocene of southern California, the latter now some 200 km north of their original position due to displacement along the San Andreas rift (Merriam, 1972), were the northern representatives of a very diverse southern (Middle American) rodent fauna, quite different from the better known faunas from farther north in the western United States. All the above localities were on or near the northern fringe of the North American tropics, and have been included in Middle America by Ferrusquía (1978: 198) who placed the northern boundary of Middle America at the 35th parallel.

The only early Tertiary (probably Eocene) rodents so far found deep within Middle America, in Guanajuato, Mexico, are not like anything known elsewhere in the continent, and thus add to the growing evidence. One, *Floresomys*, may be a sciuravid, but, if so, "is a divergent member of the family" (Black and Ste-

phens, 1973: 9); the other, *Guanajuatomys*, is a hystricognathous form that cannot at present be allocated to family (Black and Stephens, 1973: 5). Neither *Guanajuatomys* nor the likewise hystricognathous but not closely related *Prolapsus* from the middle Eocene of southwestern Texas could have been on or near the ancestry of the Caviomorpha, to judge from their cheek-tooth structure.

The Uintan *Protoptychus*, known from adjoining areas of northeastern Utah and southwestern Wyoming, was hystricomorphous and probably hystricognathous. A partial skeleton of this animal, contained in a block of hard matrix, is in the Field Museum of Natural History. The mandible, the only one known, is at present visible only in lateral view, which does not allow determination of the amount of hystricognathy that it had attained. *Protoptychus* had a tooth pattern that would have been ideally suited to have given rise to what we believe to be the primitive caviomorph type—the four-crested pattern seen in Deseadan echimyids and octodontids. We agree with Wahlert's observation (1973: 12) that the "rarity of *Protoptychus* in fossil collections supports the possibility that it, too, is based in a stock evolving elsewhere than in the western United States," which we suspect to have been in Middle America.

The earliest rodent faunas of southern California are, in general, rather similar to their contemporaries of the Rocky Mountain area, suggesting relatively little regional differentiation at that time (Golz and Lillegraven, 1977: 61 and Tables 2–3). Endemism in southern California seems to have increased fairly rapidly in the latter half of the Eocene, suggesting (Wilson, 1980: 276) that there was increased climatic differentiation at this time that led to the separation of the distinct Middle American faunas discussed above.

Berggren *et al.* (1978) have suggested that the Uintan be regarded as middle Eocene in age. The likelihood of such an age was first indicated by the discovery of *Notiotitanops*, a brontotheriid of Uintan if not Duchesnean evolutionary grade, in the marine middle Eocene Lisbon Formation in Mississippi (Gazin and Sullivan, 1942), and reinforced by Gazin's somewhat guarded observation (1955: 15) that Uintan artiodactyls were behind those of the late Eocene of Europe in their degree of advancement.

The intercalated marine and continental faunas of the San Diego area have shown that earlier Uintan continental beds are equivalent to marine middle Eocene, but that the later Uintan (equivalents of Myton or Uinta C) is upper Eocene (Golz and Lillegraven, 1977: 43 and Fig. 6). If this middle Eocene age of the earlier Uintan (Wagonhound, or Uinta A + B) be accepted, then the late early Uintan (upper Uinta B) *Protoptychus* would be middle Eocene and would have lived at approximately the time when the first caviomorphs reached South America. Some southern member or members of the Protoptychidae could have been involved in the crossing.

The recent discovery that the North American Oligocene *Cylindrodon* was at least subhystricognathous (Wood, 1980b: 6; 1981: 85–87) shows that there was another stock in the middle Eocene of Middle America (Wood, 1974a: 102–104) that may have been morphologically capable of having given rise to the Caviomorpha, although at least the Oligocene members of the family were specialized in a different direction by having acquired uniserial incisor enamel. This does not, however, seem to have been true of the middle Eocene *Mysops*, which still retained pauciserial enamel (Wahlert, 1968: 15). The middle American forms of *Mysops*, in particular, have tooth patterns that could have given rise to those of the Caviomorpha (Wood, 1973: Figs. 3–4). Unfortunately (so far as A.E.W. is aware), no specimens of *Mysops* are on record that preserve enough

of the angular process to indicate whether or not this genus showed any tendencies toward hystricognathy.

There would thus seem to have been a considerable variety of hystricognathous, and, at least in part, hystricomorphous rodents inhabiting Middle America during the latter half of the Eocene. On the basis of presently available information, this area would seem to have been the center of evolution of the Franimorpha.

It is, of course, impossible for anyone to *know* what were the dental characteristics of the ancestors of the Deseadan rodents, until such forms have been found and tied in with their Deseadan descendants by a continuous series of intermediate stages. It is easy to assume that one knows, as we have done previously, and as Hoffstetter and Lavocat have also done. Since a variety of rodents is known from the Deseadan, some must be considered more primitive than others, and each author will choose those that come closest to fitting in with his opinions as to the source of the fauna. There are genera with brachyodont cheek teeth and ones with hypsodont ones; ones in which the individual cusps are clearly distinguishable from the crests, and ones in which they are not; in each case we consider the former the more primitive, but in each case we believe that Lavocat and Hoffstetter have selected the latter. The Deseadan *Platypittamys* had cheek teeth that are among the most brachyodont of any of the known Deseadan genera, and they clearly show the presence of the individual cusps. There are only four crests, with no trace of a fifth. This is the only Deseadan rodent, whose skull is known, in which the infraorbital foramen is relatively small and the masseter either did not penetrate the foramen or did so to a very limited extent. Landry (1977: 460) stated that the infraorbital foramen of *Platypittamys* was "about the same size as that of a modern *Proechimys*, and not significantly reduced as" Wood believed. A comparison of the figures of the skull of *Proechimys*, as given by Ellerman (1940: Fig. 11) and Woods (1972: Fig. 1A) shows the foramen to be considerably larger than that of *Platypittamys* (Wood, 1949: Fig. 2A). Incidentally, Wood has never believed that the infraorbital foramen of *Platypittamys* "was significantly reduced," but rather that it was primitively small. We feel that the cumulative evidence is that *Platypittamys* and the related *Migraveramus* are the closest approaches, now available to us, to conditions in the earliest South American caviomorphs.

If we are correct as to the significance of *Platypittamys* and *Migraveramus*, the pre-South American ancestry of the Caviomorpha should be sought among four-crested hystricognathous, but perhaps not yet hystricomorphous, rodents.

Summarizing to this point, Eocene subhystricognathous and hystricognathous rodents, one or more of which are rather good structural ancestors for the Caviomorpha, inhabited North (and particularly Middle) America, the only area where such rodents have so far been definitely recorded. Members of this group could have reached Asia in the early Eocene. There was an Eocene hystricognathous radiation in Middle America. There is evidence that this area has been a faunal subregion of the continent throughout the Cenozoic (Ferrusquía, 1978). Eocene geography would appear to have been such as to have permitted rafting from North to South America in middle Eocene time.

We regard such rafting of the ancestral caviomorphs (and, presumably, platyrrhines) as being distinctly easier of accomplishment than the transatlantic crossings of over 1300 km of open water postulated by Hoffstetter and Lavocat (it would seem unlikely that winds and currents would have combined to propel rafts across the shortest possible distance between Africa and South America).

Nevertheless, their views cannot be rejected out of hand. No rafting is easy of accomplishment, which is why there is evidence of so very few successful ones. A Caribbean crossing may have been somewhat less hazardous than a transatlantic one, but this does not prove that the latter could not have occurred. Nor can the possibility, envisioned by Lavocat (1973: 166), of a latest Paleocene or earliest Eocene rafting of paramyids from Europe to Africa be summarily ruled out. More recently, Lavocat (1978: 76) stated categorically that ". . . the rodents as well as at least most of the other elements of the Oligocene fauna, are probably related to animals that reached Africa much earlier, perhaps very soon after the end of the Paleocene, and probably before the Lutetian." He also said (1978: 84), referring to an early Eocene invasion of Africa by rodents, that "such an invasion necessarily did occur. . . . At least as early as the Lutetian this . . . invasion had given rise to the first Hystricognathi with all the essential characters of that group already developing." It should be stressed that there is no direct evidence for such an early Eocene or Paleocene rodent invasion of Africa, or for the presence in the middle Eocene of Africa of fully developed hystricognaths.

Successful raftings of rodents, of the kinds and at the times postulated by Lavocat and Hoffstetter, either from Europe to Africa or from Africa to South America, must have had faunal and evolutionary consequences, and this fact permits the testing of their hypotheses against the fossil record.

Had paramyids reached Africa by the beginning of the Eocene, they would certainly have radiated rapidly in that vast continent that contained no potential competition, and would have given rise by early Oligocene time to a rodent fauna at least as diversified as that of contemporary North America. The known rodents of the *early* Chadronian of North America include 23 genera belonging to 8 or 9 families (Wood, 1980b: Table 1), in contrast to the 5 genera belonging to at most 3 closely related families from the entire Oligocene of Africa. Most recently, Lavocat (1978: 84) suggested that the thryonomyoids, bathyergoids, anomalurids and pedetids were all members of the African Eocene faunas, and proposed that all of these groups shared a common stem with the Theridomyoidea. This last idea seems extraordinarily unlikely to us; the theridomyoids are a sciurognathous but hystricomorphous middle Eocene to Oligocene European group that (unless they were related to the Anomaluridae) seem to us never to have spread out of Europe. Lavocat's suggestion of a relationship of this group of families and superfamilies appears to us to be a retreat from his belief in the fundamental importance of hystricognathy in rodent classification and a return to the acceptance of the basic importance of hystricomorphy (see below, p. 513).

Were caviomorphs the descendants of one or two successful middle Eocene raftings of African thryonomyoids to South America, one would hardly expect that, by early Oligocene time, they would have become more diversified, more numerous, and in a number of cases more specialized than their contemporary African relatives, the descendants of the stock from which they supposedly came.

The Composition of the Deseadan and Fayum Rodent Faunas

Twenty-four species of Deseadan rodents, not all formally described, representing perhaps 16 genera, have been recorded to date (Table 8). They are assignable to at least 7 families, and thus are almost as diverse as their North American contemporaries. Rodents form large percentages of the total mammalian assemblages in the better known local faunas. As noted in the Introduction (p. 374), each of these contains one rodent species that outnumbers all the rest, one

TABLE 8. RODENTS REPORTED FROM VARIOUS DESEADAN LOCALITIES.

	Patagonia				Bolivia	
	Rinconado de los Lopez	La Flecha	Cabeza Blanca	Laguna de los Machos	Salla	Lacayani
Platypittamys brachyodon	2					
Migraveramus beatus					1	
Sallamys pascuali					12	
Xylechimys obliquus				1		
Deseadomys arambourgi		1	1			
Deseadomys loomisi			1			
Scotamys antiquus		ca. 45	1			
Scotamys sp.						*
Cephalomys arcidens		12	100+			
Cephalomys plexus		1	32+			
Cephalomys sp.			1			
Cephalomys bolivianus					1	
Litodontomys chubutensis			1			
Incamys bolivianus			1		79+	
Dasyproctidae aff. *Neoreomys*					1	
Branisamys luribayensis					19	
Asteromys punctus			1	1		
Asteromys sp.						*
Chubutomys simpsoni			1			
Eocardiidae indet.			2			*
Protosteiromys medianus		7	1			
Protosteiromys asmodeophilus		2				
Caviomorpha indet.		1	1			
Octodontoidea gen. et sp. nov. 1					?	
Octodontoidea gen. et sp. nov. 2					?	
Luribayomys masticator					1	
Number of species	1	7	13	2	8–9	3
Number of specimens	2	69	144+	2	115+	*

In addition, one specimen of *Palmiramys waltheri* from Uruguay.
* Species listed by Hartenberger, 1975. Number of specimens unknown.

or two others that are moderately abundant, with the remainder represented by one or two specimens; the predominant species is different in each local fauna. At any one Deseadan locality, so far as is known, only one fossiliferous zone is represented, in contrast to the Fayum situation (see below, p. 464).

Professor E. E. Williams informed us that he had encountered rather comparable conditions in collecting Neotropical reptiles. We therefore looked for data on numbers of Recent Neotropical rodents at specific localities. These were found in the records of a plague survey carried out in northeastern Brazil from 1952–55 by the then Serviço Nacional de Peste (now Superintendência da Campanhas de Saúde Pública), in the course of which nearly 40,000 specimens of rodents were collected. Ectoparasites obtained have been published upon (Guimarães, 1972 and references therein), but almost nothing, other than the essential preliminary task of identification (by Moojen), has been done on the hosts. Arcoverde de Freitas (1957, Table 1) has given the grand totals of the forms collected in the Noreste (an unofficial name, comparable to Patagonia or New En-

Table 9. Rodents collected during the plague survey of 1952–55 in northeastern Brazil (excluding State of Bahia).

Zygodontomys lasiurus pixuna	13,486	*Echimys dasythrix lamarum*	133
Oryzomys subflavus	7056	*Oryzomys lamia*	59
Cercomys cunicularius	5700	*Calomys* sp.	50
Wiedomys pyrrhorhinos	2643	*Calomys laucha tener*	36
Akodon a. arviculoides	2213	*Oryzomys* sp.	18
Galea spixii wellsi	2137	*Proechimys guyannensis arescens*	16
Oryzomys nigripes	1944	*Dasyprocta prymnolopha*	12
Holochilus b. brasiliensis	967	*Coendou p. prehensilis*	11
Oxymycterus angularis	948	*Calomys callosus expulsus*	4
Kerodon rupestris	523	*Sciurus (Guerlinguetus)* sp.	4
Nectomys squamipes	493	*Oryzomys capito laticeps*	2
Rhipidimys masticalis cearanus	439	*Echimys* sp.	1
		Total	38,990

Data from Arcoverde de Freitas, 1957, Table 1.

gland, bestowed upon the northeastern coastal states from Maranhao to Sergipe; Bahia is not part of the Noreste), and the subtotals by Distritos, large areas that cover three to thirteen Municipios (counties). His grand totals are given in Table 9. Seventeen genera, over a third of the total recorded in the entire country (Viera, 1955) and 24 species, are represented in this comparatively small and, for the most part, far from lush part of Brazil. It is interesting to note that the 7 commonest species make up 90% of the whole, and that each of 12 species constitutes less than 1%. Arcoverde de Freitas' breakdown shows, furthermore, that relative abundance may vary widely from one Distrito to another.

A Distrito, however, is too large an area for the kind of comparison needed. For this, the lists of parasitized specimens sent by the Serviço to Dr. Guimarães have been utilized, and from them the data presented in Table 10 have been compiled. The localities (Fig. 28) have been chosen with an eye both to geographic proximity or spacing, and to the sampling of different environments. Three of the localities, G, H, and I, are single collecting stations; the rest are the combined totals for collecting stations within a Municipio.

These environments may be briefly defined (Dr. P. E. Vanzolini, personal communication) as follows:

Caatinga: rainfall 300–800 mm per annum, vegetation highly xerophytic with Cactaceae very conspicuous, soils very shallow; a harsh environment.

Agreste: rainfall 1000–1100 mm, vegetation xerophytic but Cactaceae less conspicuous, soils somewhat better; a mitigated Caatinga.

Brejo: an island of forest within Caatinga or Agreste resulting from higher elevation and increased, although locally variable, rainfall; vegetation not summer deciduous.

Atlantic Forest: rain forest with highly variable rainfall, 1200–4000 mm.

Table 10 shows that not only is the predominant species frequently different but also that relative abundances vary widely from locality to locality, even between those in close proximity, e.g., H and I (Fig. 28), or in similar general environments, e.g., E and G. Two forms, *Oryzomys subflavus* and *Zygodontomys lasiurus pixuna*, are well represented at most localities, while almost half (11 out of 23) of the species occur at only one locality. In some cases, such as B and I, two species are about equally predominant numerically. As a rule, however, one species is predominant, although not in all instances (as at A and D) overwhelm-

Figure 28. Map of northeast Brazil showing localities where rodents listed in Table 10 were collected (modified from Guimarães, 1972: Map 1). A–J: Collection localities listed in Table 10. States: 1—Piauhy; 2—Ceará; 3—Rio Grande del Norte; 4—Parahyba; 5—Pernambuco; 6—Alagoas; 7—Sergipe; 8—Bahia. Scale as shown.

ingly so. The situation at C, where *Cercomys cunicularius* is so remarkably numerous, might lead to the suspicion that a ratada, or population irruption, had been tapped by the collectors. This does not appear to be the case, since the records show peaks of abundance following the rainy season during each of the years 1952–54, which is not the classical ratada pattern. *Cercomys cunicularius* is an inhabitant of rocky places. Presumably locality C is such an area.

A general resemblance to the relative abundances encountered in Deseadan local faunas is apparent. The frequency distributions of La Flecha and Salla resemble those of localities E and G rather closely, and Cabeza Blanca shows some similarity to F. A collecting station for living forms, or a group of such stations, is of course not quite the same thing as an area in which sediments and skeletal remains are deposited. Sustained trapping will in time reveal the presence of even the rarest species and provide accurate estimates of relative abundance. The vicissitudes of taphonomy attendant upon the accumulation of a fossil assemblage, coupled with the accidents of collecting, can hardly be expected to yield precisely comparable results. Allowing for this, however, we believe that relative abundances of rodents at Deseadan localities were much like those now obtaining in Brazil (cf. Tables 8 and 10).

Deseadan caviomorphs were a rather diversified lot, ranging in size from small to fairly large (for rodents) and in crown height from brachyodont to hypselodont. Given the large numbers of the predominant forms—*Cephalomys* is the commonest Patagonian Deseadan mammal,

Table 10. Rodents collected at various localities in northeastern Brazil.

	A	B	C	D	E	F	G	H	I	J	Totals
Cercomys cunicularius[1]	4	413	1424	1	33	1				2	1878
Oryzomys subflavus	95	460		86	245	101	43	31	22	262	1345
Zygodontomys lasiurus pixuna	144	162		32	82	6	33	5	59	121	644
Akodon a. arviculoides	1						173	80	12	12	278
Oryzomys nigripes	19	12		51	3	36	11	14	67	17	230
Oxymycterus angularis	32	1			1		19	12		91	156
Holochilus b. brasiliensis	32		1		7	4	1		1	69	115
Calomys sp.				112							112
Rhipidomys masticalis cearanus	100	2					9				111
Galea spixii wellsi		13	56		2	6			1	2	80
Nectomys squamipes										39	39
Oryzomys lamia	20										20
Proechimys iheringi denigratus				19							19
Calomys laucha tener	5			13							18
Proechimys guyannensis arescens	15										15
Kerodon rupestris[2]	2	9	4								15
Wiedomys pyrrhorhinos	3	1		5					2		11
Proechimys a. albispinus				9							9
Coendou p. prehensilis	7										7
Echimys armatus	4										4
Calomys callosus expulsus				2							2
Oryzomys capito laticeps										1	1
Dasyprocta prymnolopha	1										1
Total											5110

Localities, here and on Fig. 28, are: A. Ceará, Municipio de São Benedito, Brejo; B. Pernambuco, Municipio de Triunfo, Brejo; C. Pernambuco, Municipio de Bodocó, Caatinga; D. Bahia, Municipio de Vitoria da Conquista, transitional between Caatinga and Atlantic Forest; E. Alagoas, Municipio de Palmeira dos Indios, Agreste; F. Alagoas, Municipio de Limoeiro de Anadia, Agreste; G. Pernambuco, Municipio de Caruaru, Fazenda Caruaru, Agreste; H. Pernambuco, Municipio de Garanhuns, Sitio Barrocão 3°, Atlantic Forest with areas of Agreste; I. Pernambuco, Municipio de Garanhuns, Fazenda Cristovão, Atlantic Forest with areas of Agreste; J. Alagoas, Municipio de Viçosa, Atlantic Forest.

[1] *C. c. inermis* at D; *C. c. laurentius* at the other localities.

[2] An inhabitant of rocky places, this species is perhaps under-represented.

Rattus and *Mus*, some of which were taken, have been excluded.

Determinations by J. Moojen. Certain nomenclatural emendations were made by B.P.

Incamys apparently the commonest Bolivian one—we suspect that by early Oligocene time the caviomorphs were well on the way toward achieving the numerical position and ecological diversity in the South American mammalian fauna that is held by rodents today. In the rich Santacruzian fauna of early Miocene age (21.7–18.5 m.y.b.p.; Marshall *et al.*, 1977) there are only 19 genera of rodents. Scott (1905), largely following Ameghino, a splitter of the first order, listed nearly 70 species, surely too high a number. Revision at the specific level has yet to be done. Data sufficient for any attempts at numerical analyses of the fauna are not available in the literature.

The Fayum thryonomyoids present quite a different picture. Three levels in the Jebel el Qatrani Formation yield mammalian remains: the lower fossil wood zone, the Yale Quarry G level, and the upper fossil wood zone; the lower and middle horizons are separated by an interval of 140 feet, the middle and upper by one of 150 feet (Simons, 1968: 21). The time involved in the deposition of these deposits apparently spanned most of the Oligocene (Simons, 1968: 4).

The rodents from this sequence com-

TABLE 11. THE FAYUM RODENT FAUNAS.

	Lower fossil wood zone (Quarries A, B, E)	Quarry G	Upper fossil wood zone (Quarry I)
Phiomys andrewsi	30	2	
Phiomys lavocati	9		
Phiomys paraphiomyoides		6	
Phiomys aff. *paraphiomyoides*			4
Phiomys or *Metaphiomys* sp.	2	6+	
Metaphiomys schaubi	6	59	
Metaphiomys beadnelli			2
Cf. *Metaphiomys* sp.	1		1
Phiocricetomys minutus			1
Gaudeamus aegyptius	11		
Neosciuromys simonsi			1
Unidentified		113+	9
Number of species	6	4	5
Number of specimens	59	186+	18

Data essentially from Wood (1968). The unidentified specimens have been recorded by Conroy (1976: 20) for Quarry I and by Simons (personal communication) for Quarry G; all were collected since 1968. Since this table was prepared, a collection in the MCZ of about 120 isolated cheek teeth and 1 lower jaw fragment, sorted from matrix from Quarry G, has become available. The jaw and 53 cheek teeth are referable to *Phiomys*, the remainder to *Metaphiomys*.

prise 8 to 11 species (3 possibly distinct forms were not named) representing 5 genera (Table 11) and 3 families. Wood (1968) placed all forms in one family, the Phiomyidae, a step justified on the basis of their morphological similarity. Lavocat (1973: 20), in agreement, pointed out that familial separation is only made possible by better knowledge of their Miocene descendants. We have previously stated (1959: 389) that Deseadan caviomorphs formed a relatively homogeneous group. This they did, but they were very much more diversified morphologically than their Fayum contemporaries. The much greater homogeneity of the Fayum than of the Deseadan rodents, and the fact that they were, individually, of smaller size, makes it difficult to understand the statement by Lavocat (1969: 1497) that the South Atlantic "a joué un rôle de filtre important, la faune de Rongeurs qui a réussi à passer en Amérique du Sud étant beaucoup moins variée que la faune autochthone d'Afrique, et constituée semble-t-il essentiellement par de petites formes arboricoles."

Table 12 compares the numbers of mammalian species collected by Loomis' expedition to Cabeza Blanca, Patagonia, with the numbers collected in one quarry (Quarry I) in the upper fossil wood zone of the Fayum during several field seasons. The difference between the two in the percentage of rodents is striking. At neither locality are the sediments uniform, and as regards the total number of specimens collected the two are not very different. Cabeza Blanca is a small hill, about 240 m long and averaging about 60 m in width, capped over much of its extent by the Miocene Monte Leon ("Patagonian") Formation; the Deseadan sediments there are 12.7 m thick (Loomis, 1914: 6, 21). Quarry I measures roughly 100 by 50 m and the sediments are about 1 m thick (E. L. Simons, personal communication). All matrix in Quarry I was meticulously examined, whereas no quarrying was carried out at Cabeza Blanca, all specimens collected having been found on the surface or in the process of weathering out. To compare the two seems fair, and it is clear that rodents

Table 12. Comparison of Patagonian and Fayum local faunas.

Cabeza Blanca			Jebel el Qatrani, Quarry I		
	N	%		N	%
Notoungulata	125	44.3	Artiodactyla	147	38.3
Rodentia	102	36.1	Primates	105	27.2
			Hyracoidea	72	18.6
Edentata	23	8.5	Creodonta	22	5.2
Litopterna	15	5.3	Rodentia	18	4.7
Marsupialia	11	3.9			
Astrapotheria	6	2.1	Proboscidea	8	2.1
Condylarthra	1	0.4	Chiroptera	6	1.1
			Insectivora *s.l.*	3	0.8
Total	283		Sirenia	3	0.8
			Embrithopoda	2	0.5
			Total	386	

Numerical data for Cabeza Blanca from Loomis (1914: 19–20, 216); for Quarry I from Conroy (1976: 20, 22). All specimens identifiable to order—cranial, postcranial and dental—are counted. Of the Cabeza Blanca notoungulates, 31 (24% of the members of that order) are comparatively small, rather rodent-like members of the suborders Typotheria and Hegetotheria.

really are far less abundant at Quarry I than at Cabeza Blanca; it may be added that five other Yale quarries in the upper fossil wood zone contained no rodent remains at all. Had the large forms, arsinoitheres and gomphotheres, been better represented in Quarry I, the percentage of rodents would have been still lower. The Cabeza Blanca faunule is more nearly a representative sample of the ambient mammalian fauna; in Loomis' collection the smaller mammals constitute about 59% of the whole, medium-sized ones about 16%, and large ones 25%.

As regards the other Fayum levels, the lower fossil wood zone has yielded 59 specimens of rodents. This is the longest worked of the Jebel el Qatrani horizons, and Professor Simons is willing (personal communication) to estimate that about 2000 specimens of mammals have been collected from it. Taking this estimate, rodents constitute roughly 3% of the whole, despite the concentration of the Yale parties on finding the smaller faunal elements, which resulted in their increasing the number of known rodent specimens from the zone nearly fivefold.

In the middle Jebel el Qatrani, at Quarry G, the fossiliferous bed is homogeneous, 14 m long, 1 m wide and 4 cm thick at the center, tapering to feather edges at the sides, evidently what remained of the bed of a small stream. Except for one tooth of *Moeritherium* and one of an anthracotherid, the mammals are all small (E. L. Simons, personal communication). Here, rodents constitute about 58%, primates 27%, hyracoids 10%, creodonts 3% and "insectivores," *s.l.*, 1% of the total. The stream evidently ran through or near a habitat congenial to *Metaphiomys schaubi*, by far the commonest species in the deposit. Apart from a maxillary fragment of *Phiomys paraphiomyoides* found about a meter above the quarry, no other fossils were found near Quarry G (G. Meyer, personal communication). Quarry G is obviously a special case.

The available data indicate quite clearly that the rodents of the Jebel el Qatrani were on the whole less numerous relative to their contemporaries than were those of the Deseadan.

Passing on to taxonomic diversity, there is a paucity of rodent species in each of the three levels—6 in the lower fossil wood zone, 4 in Quarry G, and 5 in

the upper fossil wood zone, compared with 13 recorded from one level at Cabeza Blanca. The difference in total taxonomic diversity is striking—7 families, perhaps 16 genera and 24 species in the Deseadan as against 3 families, 5 genera and 8 to 11 species in the Fayum, a point touched on by Hartenberger (1975: 429). This indicates to us that caviomorphs had been evolving considerably longer in South America than had thryonomyoids in Africa.

The Fayum and Deseadan rodent faunas are far apart as regards structural diversity. All Fayum rodents are small, except *Neosciuromys* (*"Paraphiomys"*) *simonsi* (see below, p. 520), which was only as large as *Ondatra* or *Cynomys*. The Fayum rodents, in their entirety, are more specialized than any Oligocene rodents from any other part of the world in their marked degree of retention of dm_4^4, a character not met with in any known Deseadan rodent (this and other dental differences are discussed at length below, pp. 491–503). On the other hand, the Fayum thryonomyoids are far behind many Deseadan caviomorphs in cheek-tooth height. Nearly all of them are brachyodont, only *Neosciuromys* and *Gaudeamus* being incipiently mesodont. In the Deseadan, *Protosteiromys* is brachyodont; *Platypittamys* and *Migraveramus* are essentially brachyodont; *Sallamys* and *Branisamys* are brachyodont with incipient unilateral hypsodonty; *Deseadomys, Xylechimys* and *Asteromys* are mesodont, the first with some unilateral hypsodonty in the uppers (the other two are known only from parts of mandibular rami); *Cephalomys* and *Incamys* show marked unilateral hypsodonty, especially in the uppers; *Litodontomys* and *Chubutomys* (both known only from parts of mandibular rami) are hypsodont; and *Scotamys* is hypselodont. In cheek-tooth structure the Deseadan caviomorphs are much more varied than the Fayum thryonomyoids, and several of them are considerably larger. All this likewise suggests that caviomorphs had been resident in South America longer than had thryonomyoids in Africa.

There is one outstanding fact concerning the Fayum faunas: of all the rodents in the Yale and other museum collections, not one is attributable to any group other than the Thryonomyoidea. Lavocat (1973: 196, 252) reported that Simons had shown him an ulnar fragment from the upper levels of the Jebel el Qatrani Formation that was unquestionably that of an anomalurid. Search of the Yale collections has uncovered no trace of such a fragment. Simons informs us (personal communication to B.P.) that he has no recollection of ever having seen such a specimen, of ever having shown it to Lavocat, or of having Lavocat tell him that it was an anomalurid. Lavocat (1978: 80) stated, of anomalurids, that "their Oligocene record is extremely poor except for the Fayum ulna." This statement suggests that there is more basis for assuming that there were Oligocene anomalurids in Africa than is supported by the evidence, since the Oligocene record of anomalurids (except for the supposed Fayum ulna) is nonexistent.

If we contrast the Fayum assemblage with that present in one North American early Oligocene local fauna, the Porvenir Local Fauna in the Chambers Tuff Formation of southwestern Texas, we note that the latter includes 6 families of rodents, one represented by 3 and two others by 2 subfamilies; perhaps 13 genera; and some 15 species—and all this diversity is revealed by a total of only 44 specimens (Wood, 1974a: Table 1). To us it is inconceivable that, if primitive rodents had made a landfall on Africa in latest Paleocene or earliest Eocene, as proposed by Lavocat (1973: 166), so few rodent species, all of them members of one closely knit group, would occur in three levels of a formation laid down, during most of the Oligocene, at least 16 m.y. after such a landfall. Rodents do not evolve so slowly, especially in the com-

TABLE 13. RODENTS FROM THE EARLY MIOCENE OF EAST AFRICA.

Old natives (Thryonomyoidea)		Recent immigrants (all others)	
Diamantomys luederitzi	2180 + abundant at 3 levels of Napak	*Paranomalurus soniae*	70
		Bathyergoides neotertiarius	62 + "4 boites"
		Afrocricetodon s. songhori	65
		Megapedetes pentadactylus	53 + incisor fragments
Paraphiomys pigotti	1734		
Paraphiomys s. stromeri	110	*Paranomalurus bishopi*	51
Simonimys genovefae	46	*Vulcanisciurus africanus*	32
Phiomys cf. *andrewsi*	23	*Notocricetodon petteri*	21
Paraphiomys stromeri hopwoodi	20	*Paranomalurus walkeri*	20
Myophiomys arambourgi	19	*Proheliophobius leakeyi*	14
Epiphiomys coryndoni	14	*Protarsomys macinnesi*	9
Thryonomyoidea indet.	12	*Afrocricetodon songhori korui*	5
Kenyamys mariae	9	*Afrocricetodon* sp. 2	4
Elmerimys woodi	3	Sciuridae gen. et sp. indet.	3
Andrewsimys parvus	2	*Megapedetes* sp.	3
		Zenkerella wintoni	2
		Afrocricetodon sp. 1	1
Total counted specimens	4172	Total counted specimens	415
Percent of grand total	90.95%	Percent of grand total	9.05%
9 genera, 11 species or subspecies		10 genera, perhaps 16 species or subspecies	

Numbers based on the maximum figures given by Lavocat (1973). Specimens without precise locality, cited merely as "Kenya" are included, but those from Kirimun and "Lodwar" are excluded. The "4 boites" of *Bathyergoides neotertiarius* are of necessity not included.

plete absence of any competition. We must conclude, therefore, on the available evidence, that Lavocat's hypothesis of a very early date of arrival of rodents in Africa must be rejected.

To what extent the Fayum rodents were representative of the early Oligocene rodent fauna of the African continent is a question that must now be considered. Conditions prevailing during the deposition of the Jebel el Qatrani Formation—rivers, streams, lakes, ponds, forests and, possibly, savannah (Simons, 1968: 15–16)—would certainly seem to have been suited to the support of a rodent fauna at least as varied as that of Cabeza Blanca (cf. Tables 8 and 10), had such been in existence in Africa at the time.

Comparisons of the Fayum faunas with those of the late Burdigalian deposits of East Africa are instructive in this connection. Table 13 lists numbers of specimens of all East African rodent taxa, and the percentages that belong to the Thryonomyoidea and to the other rodent families and superfamilies that had, in the early Miocene, only recently invaded the African continent.

In the compilation of Tables 13 and 14 we have utilized the numbers of specimens enumerated by Lavocat (1973) under the taxonomic headings in the main body of his text, and those listed in his summary table on page 245 of that work. These two sources often disagree; in fact, they conflict over half the time. Most of the discrepancies are minor, but some are glaring. For example, 70 specimens of *Paraphiomys pigotti* and 48 of *Diamantomys luederitzi* from Rusinga are enumerated in the text (Lavocat, 1973: 22–23, 52), whereas 487 and 1647, respectively, are listed in the table; for *D. luederitzi*, 74 are enumerated from Songhor, but 1104 are listed in the table, although the text also specifies "nombreux autres échantillons" of upper teeth of *D. luederitzi* from Rusinga and Songhor (Lavocat, 1973: 52). Since specimens of upper

TABLE 14. NUMBERS, PERCENTAGES OF TOTAL RODENTS, AND NUMBERS OF TAXA OF RECENT IMMIGRANT RODENTS IN THE EARLY MIOCENE OF EAST AFRICA.

	Number of specimens	Percent of total rodents	Genera	Species & subspecies
Bathyergoidea	76 + "4 boites"	1.66	2	2
Anomaluridae	143	3.12	2	4
Pedetidae	56	1.22	1	2
Cricetidae	105	2.29	3	6
Sciuridae	35	0.76	2	2
Total	415	9.05	10	16

The "4 boites" of Bathyergoidea have of necessity been omitted from the calculations.

teeth of fossil rodents are usually distinctly rarer than those of the lowers, the fact that Lavocat lists only 28 specimens of lower teeth of this form from Songhor and 22 from Rusinga strongly suggests that the "nombreux autres échantillons" totalled significantly less than the 50 specimens of lower teeth. Lavocat's table (1973: 245) states that *Diamantomys luederitzi* is "Abondant" at three of the four levels of Napak, whereas, on page 52, he enumerates only 31 specimens from that locality. In the list of referred specimens of *Bathyergoides neotertiarius* (Lavocat, 1973: 110), there are included (in addition to 33 listed specimens) "4 boites" from Songhor, that we have perforce neglected in our calculations. Lavocat's table (1973: 245) merely lists this species as being "Abondant" at Songhor. In all cases of conflict we have used the higher of the numbers given by Lavocat. Even so, our Table 13 is clearly not complete. Lavocat enumerated, in his text, a total of 76+ rodent specimens from Napak, whereas Bishop (1967: 48) recorded 716 as having been collected there between 1958 and 1965. We must assume that these presumably unstudied specimens would not materially change the relative abundances shown by our Tables 13 and 14.

Numerically, the old natives (Thryonomyoidea) greatly outnumber the invaders (4172 to 415), the latter constituting only 9% of the total (Table 13). As regards taxonomic diversity, the invaders have an edge, 10 genera and 16 species or subspecies, as against 9 genera and 11 species or subspecies of thryonomyoids. This diversity results from the then-recent establishment of a land connection with Eurasia. In the early Miocene of East Africa we are witnessing the irruption of already differentiated southwest Asian faunal elements, that had not yet succeeded in dominating the autochthonous African rodent fauna. Lavocat (1973: 247) suspected that the invading cricetids had differentiated prior to their arrival in Africa; we go farther, suspecting that this was the case for all the non-thryonomyoid families, each of which was contributing an approximately equal amount to the total rodent fauna (Table 14). *Diamantomys luederitzi* and *Paraphiomys pigotti* constitute 85% of the total specimens; the eight commonest forms make up well over 90% (almost 95%), and the remainder, 17 in all, each contribute less than 1%.

Here in the early Miocene we see rodent faunas in full flower, as in the Deseadan of South America. The resemblance to the Recent faunas in the Brazilian Noreste (Tables 9, 10) is rather close, and the contrast to the Fayum rodent faunas is striking.

Lavocat (1973: 246), on the basis of differences in relative abundance of certain

Table 15. Ordinal percentages in early Miocene faunas of East Africa.

	Songhor	Koru	Mfwangano	Napak
Rodentia	82.5	86.5	68.6	64.0
Proboscidea	—	—	0.3	10.9
Artiodactyla	10.8	3.9	16.5	9.3
Primates	2.5	4.3	3.0	6.0
Others	4.1	5.3	11.6	9.8

Data from Bishop (1967: 48) for Napak (four levels lumped); from Bishop and Whyte (1962: 1286) for the other three. Cranial and dental specimens only.

rodent species, has tentatively suggested that the East African early Miocene fauna of Rusinga might be a little older than that of Songhor. As the Brazilian data show, this conclusion does not follow.

The early Miocene rodents of East Africa had achieved the numerical predominance (Table 15) characteristic of the order in areas where it has become well established, due primarily to the successful diversification of the thryonomyoids during the 10 m.y. of the Oligocene. That the Fayum thryonomyoids were far from having achieved such a position would seem evident (cf. Tables 12 and 15).

Under the circumstances, we are forced to conclude, for all the reasons discussed above, that the Fayum rodents were indeed representative of the early Oligocene rodent fauna of Africa.

The degree of diversity and numerical abundance attained by the Fayum thryonomyoids, whether placed in one family as was done by Wood (1968), in three closely related families as we do here, or in four as was done by Lavocat (1973: 160), was certainly no greater and probably less than that of the Recent Australian murids. These rodents belong to three subfamilies, the Murinae of Asian origin, the Hydromyinae and the Pseudomyinae. The Hydromyinae originated in New Guinea, the Pseudomyinae in Australia (Tate, 1951: 217–221), the two areas having been separated a significant portion of the later Tertiary. Intermigrations occurred during Pleistocene periods of low ocean levels. A single rodent incisor has been reported from the Pliocene Otibanda Formation of New Guinea, dated at 5.7–7.6 m.y.b.p. (Plane, 1967: 56). In Australia, the "Pseudomyinae differentiated, spreading into all the usual rodent niches, including burrowing (*Mastacomys*), saltatorial (*Notomys* and, partially, *Conilurus*) and arboreal (*Mesembriomys* and, partially, *Conilurus*), as well as the more typical scampering niche . . ." (Wood, in press, b).

Isolated pseudomyine molars have been reported from the Pliocene Chinchilla local fauna of southeastern Queensland, dating from about 4 m.y.b.p., and a single rodent incisor was found in the slightly older (4.5 m.y.b.p.) Bluff Downs Formation of northern Queensland (Archer and Bartholomai, 1978: 15–16), but no rodents are included in the extensive microfauna of the Hamilton Formation of Victoria, dated at 4.3 m.y.b.p., in spite of extensive sieving (Turnbull and Lundelius, 1970; Archer and Bartholomai, 1978: 15). This strongly suggests that the rodents had only just reached northern Australia in Bluff Downs time, and that their apparent absence from the Hamilton fauna represents a real absence from the southern border of the continent at that time (Archer and Bartholomai, 1978: 15; Turnbull, personal communication; Wood, in press b). The success of introduced rabbits in Australia should be a clue as to how rapidly rodents would have spread when they reached Australia (or the equally island continents of Eocene South America and Africa).

"That is, the present diversity of the Pseudomyinae represents the maximum differentiation that members of this rapidly reproducing and rapidly evolving order could achieve, in an area of continental size, with no real competition of any kind, in about 4.5 million years" (Wood, in press b).

The comparison of the diversification

of the Fayum thryonomyoids with that of the Australian pseudomyines strongly implies that rodents had been in Africa no more (and probably significantly less) than 4.5 m.y. before the deposition of the lower fossil wood zone. This would mean that rodents first reached Africa no earlier than late in the Eocene. The much greater diversity and abundance of the Deseadan caviomorphs is in accord with their having been in South America two or three times as long, probably having reached South America 10–12 m.y. before the Deseadan, presumably immediately after Musters time (Wood, in press b). Therefore, derivation of the Caviomorpha from the thryonomyoids would appear to us to be an untenable hypothesis.

As we have pointed out before (1959: 397, n. 32), if transatlantic rafting of rodents had occurred, on faunal grounds it would be more likely to have been from South America to Africa. Now as then, we do not take this possibility seriously. Platyrrhine primates also make their first appearance in the Deseadan, and it is not surprising that a nearly identical gamut of opinions regarding their dispersal has been run. Hoffstetter (e.g., 1972) has advocated rafting from Africa, while Szalay (1976: 426) has suggested rafting in the reverse direction. In answer, Hoffstetter (1977) cited the much greater abundance and diversity of the Fayum primate fauna as a telling argument against such a view. He is quite right—and precisely this same argument is equally valid evidence against the possibility of a rafting of thryonomyoids to South America. Relationships and place of origin of the platyrrhines are open and lively questions. Transatlantic rafting of the ancestral stock is perhaps a little less unlikely than rafting of ancestral caviomorphs (there is not so much evidence against it), and so cannot be ruled out entirely. Nevertheless, we adhere for the present (Wood, 1981) to the third and older alternative, that catarrhines and platyrrhines have descended from a common ancestral stock that lived in the southern parts of the northern hemisphere, and which reached Africa and South America independently. For further discussion of the difficulties involved in transatlantic rafting, see Simons (1976), who has informed us (personal communication) that in his opinion such resemblances as exist between the Deseadan primate *Branisella* and the Fayum primates are of a general nature and indicate no special affinities.

With that, we may proceed to a consideration of certain other items of evidence that have been cited to support a thryonomyoid ancestry for the caviomorphs.

The Evidence from Parasitic Nematodes

Hoffstetter (e.g., 1975: 522–523) and Lavocat (1973: 256) have indicated that evidence from certain parasitic nematodes favors an African origin for the Caviomorpha. Use of the data from these parasites is complicated by the complete absence of a fossil record to provide a time scale for nematode evolution, by the fact that there are probably very large gaps in our knowledge of present-day nematodes and their distribution, and by the fact that it is as difficult for paleontologists to interpret the data from parasites as for parasitologists to interpret those from fossils. Nevertheless, since nematodes have been cited to support thryonomyoid-caviomorph relationships, we have ventured into this gray area of interpretation, feeling that, at least, we can speak on the subject with as much authority as do Hoffstetter and Lavocat.

The nematode groups in question are the Heligmosomidae (Durette-Desset, 1971) and the Oxyurinae of the Family Oxyuridae (Quentin, 1973a, 1973b, 1973c).

Durette-Desset's concept of the Heligmosomidae would seem to be that of a grade rather than a clade, since she evidently believed (1971: Figs. 95–96) that

the evolutionary "lignées" (all but one consisting of separate subfamilies) arose independently from different genera of the ancestral Family Trichostrongylidae, and developed their heligmosomid features as parallelisms. The major host group is the Rodentia, heligmosomids being reported in 17 of the living families.

Among Old World hystricognaths, *Thryonomys* is infected by *Heligmonella* (Heligmonellinae), the hystricids by *Heligmonella* and by *Paraheligmonina* (Brevistriatinae) in Africa and by *Cordicauda* (Brevistriatinae) in the Oriental Region, and the bathyergids by *Ortleppstrongylus* (Impalaiinae). There are no records for *Petromus*.

Within the caviomorphs, there is a sharp cleavage. Cuniculidae, Caviidae, Hydrochoeridae and Chinchillidae harbor *Vianella* (Vianniinae) whose other hosts are didelphids; presumably a transfer from the latter to the former was involved here. Echimyidae, Dasyproctidae and Erethizontidae are afflicted by members of the Subfamily Pudicinae, the echimyids by *Pudica*, *Heligmostrongylus* and *Pseudoheligmosomum* (Capromyinae, only, for the last), the dasyproctids by *Pudica* and *Heligmostrongylus*, and the erethizontids by *Heligmostrongylus*. In addition, *Paraheligmonella* (according to Durette-Desset, 1971: 50, the reference of this genus to the Heligmonellinae is questionable) has been recorded from the echimyids *Cercomys* and *Capromys*, and a species of *Stilestrongylus* (Nippostrongylinae), a genus otherwise confined to Neotropical cricetids, occurs in an echimyid, presumably another case of transfer. Heligmosomids have not been reported from the Octodontidae, Abrocomidae or Dinomyidae.

Durette-Desset doubted that host specificity is of primary importance in the Heligmosomidae, believing, rather, that diversification of the family came about mainly by various evolutionary "bursts" that accompanied expansion of suitable host groups. She postulated that heligmosomids were not in existence in the Paleocene (1971: Fig. 86), the various "lignées" having arisen during the Eocene. The "lignée" of interest in the present connection is that of *Heligmonella*. From the Subfamily Heligmonellinae there arose, in the late Eocene or early Oligocene according to Durette-Desset, the Pudicinae in South America and the Brevistriatinae in the Old World, and, in the later Tertiary, coinciding with the rise of the Muridae, the Nippostrongylinae. With the exception of *Paraheligmonella* in certain echimyids, the heligmonellines are Old World in distribution (Palaearctic talpids, Palaearctic and Oriental lagomorphs, and an Oriental sciurid in addition to *Thryonomys* and African hystricids).

However, Durette-Desset (1971: 50) apparently considered it uncertain as to whether *Paraheligmonella* was actually a heligmonelline. "Le fait que nous classions ce genre dans la même sous-famille qu'*Heligmonella* (mais en le considérant comme un peu plus évolué) implique une invasion de l'Amérique du Sud par les Rongeurs africains. Nous devons insister sur la fragilité de notre hypothèse, puisqu'elle ne repose que sur la structure du synloph. D'autres éléments, au contraire, sont déjà assez charactéristiques de la faune sud-américaine (division de la dorsale, arêtes discontinues)." It is this very, very tentative suggestion, that the subfamily crossed the South Atlantic inside rafted thryonomyoids, that Lavocat and Hoffstetter have emphasized.

Other interpretations would seem possible. In the first place, as we understand Durette-Desset's reservations, it seems entirely possible that her very tentative reference of *Paraheligmonella* to the Heligmonellinae may be incorrect, and that the features uniting *Paraheligmonella* and the Heligmonellinae evolved as parallelisms, an amount of parallelism apparently no greater than that which she accepts in the parallel evolution of the

subfamilies from the ancestral Trichostrongylidae. If so, heligmosomid support for transatlantic rafting collapses at the outset. Secondly, we do not see that there is any basis for assuming that the heligmosomids were not in existence during the Paleocene, especially since didelphid marsupials and insectivores, two other groups parasitized by them, were then present, and remembering the lack of host specificity that Durette-Desset stresses. In discussing the relationships between heligmosomid evolution and rapid radiations of host groups, Durette-Desset has omitted the most important rodent evolutionary "burst" of all, the protrogomorph-franimorph radiation of latest Paleocene and early Eocene time. Rodents being the major host group (approximately 80% of the species listed by her infest members of this order), it seems unlikely to us that heligmosomids would not have profited from this radiation. We suggest, therefore, as an alternative possibility, that heligmonellines arose in Paleocene time in Holarctica, parasitized the ancestral hystricognath infraorder Franimorpha and their descendants, and subsequently gave rise to the Pudicinae in South America and to the Brevistriatinae in the Old World. *Paraheligmonella*, if correctly referred to the Heligmonellinae, would be, in this view, a surviving New World heligmonelline, not a transatlantic immigrant from the Old World.

In passing, it may be stressed that bathyergids are parasitized by members of the Subfamily Impalaiinae, which does not infest any other Old World hystricognaths. We believe that this was considered by Durette-Desset to be the most primitive of the "lignées"; she indicated that the subfamily originated in the middle Eocene (1971: 98), and in her phylogenetic chart (1971: Fig. 95) she shows this as the left hand "lignée." If Lavocat was correct (1973: 256) in his opinion that the distribution of nematodes is a key to host interrelationships, we feel that these data should have given him pause in attempting to derive the Bathyergoidea from the Thryonomyoidea (1973: 150–153).

In the case of the Oxyurinae, the major host group is again the Rodentia; members of 13 families are at present known to be infested by oxyurines. Other hosts, so far as recorded, are: Marsupialia (Australia only), Dermoptera, Lemuroidea, Platyrrhini, Leporidae and selenodont Artiodactyla. This is a very mixed bag, which suggests that knowledge of the distribution of the subfamily may be far from complete. No oxyurines have so far been recorded for either *Thryonomys* or *Petromus*. Four genera—*Hilgertia*, *Heteromyoxyuris*, *Helminthoxys* and *Evaginuris*—are of interest in the present connection.

Hilgertia, which is not very closely related to the others (Quentin, 1973c: Figs. 21, 23–24), is known from *Ctenodactylus* and *Heterocephalus*. Ctenodactylids were certainly of Asian origin (Wood, 1977a) and we believe bathyergids were, as well (see below, p. 516).

The other three genera, which form a closely related group, are, with the possible exception of two species of one of them, New World forms. *Heteromyoxyuris* infests heteromyids, a North American family which does not, as Quentin stated (1973c: 1092), date from the early Eocene but from the early Oligocene.

The various species of *Helminthoxys* are divided by Quentin (1973c: 1081) into four "lots." The first of these infests *Lagidium*, the second *Capromys*, the third *Microcavia* (*"Caviella"*), and the fourth *Dasyprocta* and *Cercomys*. Relying on our diagram (1959: Fig. 34) of caviomorph relationships that hypothesized early Miocene dates of origin for the Caviidae and the Capromyidae (in which, following a consensus, we then included the myocastorines), Quentin suggested (1973c: 1092) that infestation of these by two of the principal "lots" of *Helminthoxys* "indiquerait effective-

ment une évolution plus récente de ce genre." This may have been the case, but we know of no reason why the caviids could not have inherited these parasites from the extinct, broadly ancestral Eocardiidae. The Capromyinae, as we now restrict them (p. 393), are unknown prior to the Antillean late Quaternary. The other two families harboring species of this genus, like the Eocardiidae, go back to the Deseadan, so there seems to be no reason why *Helminthoxys* could not date at least from the early Oligocene.

Species of *Evaginuris* have been recorded, in the New World, from *Erethizon*, *Coendou*, and *Dinomys*. The type species, the North American *Evanginuris compar*, has been found in the domestic cat (the source of the type material) and in *Odocoileus*, as well as in *Erethizon dorsatum* and *E. epixanthum*. With this distribution, one wonders where else the species may occur. Interest here, however, centers on the two Old World reports of species of this genus.

Evaginuris evoluta (von Linstow) was originally—and summarily—described as a new species of *Oxyuris* (von Linstow, 1899: 20). When Quentin examined the type material, he found it to be "en mauvais état," "3 femelles desséchées, en fragments . . . . Ce matériel a pu être réhydraté en partie . . . par le procédé du phosphate monosodique" (1973c: 1068). How much of the original structure is recapturable by this technique is not for non-specialists to say. However, there is some uncertainty as to the provenance of these fragments, although Quentin (1973a: 2015) cited *E. evoluta* as "parasite d'un *Hystrix brachyura* originaire de Malaisie." Von Linstow, however, merely listed "*Hystrix brachyura* (?)*" without further details, although for other species of nematodes that he described in the same paper he was meticulous in recording localities and collectors. He added, in the footnote: "*Manuscriptname, dessen Identität nicht mehr festzustellen ist." We are thus left with unanswered questions. Was von Linstow in doubt as to whether the manuscript name, i.e., the host datum, was correctly associated with the caecum in which he found the oxyurine specimens, or was it the identification of the host that he questioned? If the host datum was essentially correct, could the animal have been a zoo inmate, housed in a cage adjacent to that of, perhaps even shared with, some erethizontid?

A second species of *Evaginuris*, *E. stossichi* (also originally referred to *Oxyuris*), has been reported from *Hystrix cristata* (Quentin, 1973a: 2015). Again, there seem to be problems with this species, which was originally given a very incomplete description (Quentin, 1973b: 1403). In 1956 "Vuylsteke . . . identifie à nouveau l'espèce chez un *Hystrix cristata* du Jardin Zoologique d'Anvers . . ."; these specimens were studied by Quentin and were the basis for his transferral of the species to *Evaginuris*. Since this specimen of *Hystrix cristata* was definitely a zoo inmate, the question raised above about the source of the *Evaginuris evoluta* infestation is equally applicable here.

We cannot answer the questions we have raised, but it seems obvious to us that the records are somewhat suspect, and that they should be confirmed from field collected specimens before they can be accepted at face value.

Even should the records be confirmed, there would be no necessity to invoke transatlantic rafting to account for the occurrence of *Evaginuris* in New and Old World porcupines. Quentin believed that *Evaginuris* was descended from *Heteromyoxyuris* or something very similar. The presence of this last genus in the wholly American (and, in the Oligocene, exclusively North American) Heteromyidae argues strongly that members of this group of oxyurine genera were present in the North American Eocene. They could not have been parasites on the Heteromyidae, nonexistent at that time. Some

extinct family or families of rodents were presumably involved. If these had a Holarctic distribution, *Heteromyoxyuris* and, very possibly, *Evaginuris*, also had a similar distribution, and could have independently transferred to Asian hystricid descendants of the ancestral rodent hosts, as well as to Middle America, where they would have been ready to migrate to South America with the ancestral caviomorphs. It seems to us that those who are not willing to accept this view must face the difficult paleobiogeographic problem of explaining how the ancestral *Evaginuris* was able to reach the Old World tropics after having evolved from the North American *Heteromyoxyuris*.

Furthermore, if it is proposed that the distribution of *Evaginuris* be considered a support for the hypothesis of the derivation of the Caviomorpha from the Thryonomyoidea, it seems most surprising to us that the Old World members of *Evaginuris* should be confined to hystricids, absent from Africa, so far as anyone knows, until late Tertiary, and be unknown in the thryonomyoids, the group some of whose members supposedly crossed the South Atlantic carrying *Evaginuris*.

In summary, the evidence from nematodes cited as favoring transatlantic rafting is shaky indeed, and the support it offers for an African origin of the Caviomorpha has been grossly exaggerated. Further, even if the evidence for close relationships of the nematodes of caviomorphs and Old World thryonomyoids were accepted as being as clear-cut as indicated by Hoffstetter (1975: 522–523) and Lavocat (1973: 256), the data are capable of other, at least equally plausible, interpretations.

Comparisons of Caviomorpha and Old World Hystricognathi

We may now pass to a consideration of the hystricognathous rodents themselves, investigating the resemblances between the New and Old World forms. The points of similarity are numerous, which of course accounts for the controversies that have raged about the degree of relationship. There are three questions. First, which of these similarities are confined to the Caviomorpha and the Old World hystricognaths, and which are found as well in one or more of a variety of sciurognathous rodents? Secondly, which features are found in the North American Eocene hystricognaths, and which are limited to the Oligocene and later caviomorphs and Old World hystricognaths? Thirdly, are the resemblances that are confined to the Oligocene and later hystricognaths of so overwhelming and so exclusive a nature as to demand direct descent of the caviomorphs from hypothetical middle Eocene African thryonomyoid ancestors, or could they be the results of independent descent from a common, northern hemisphere franimorph ancestry combined with parallel evolution occurring subsequent to geographic separation? We shall discuss the answers to the three questions together.

(1) *General.* Lavocat (1973: 168) has listed, without discussion, 16 "principal common characters" of the Old World hystricognaths (his Phiomorpha) and the Caviomorpha. We believe that he omitted discussion because he had recently covered some or all of these points in detail (Lavocat, 1971a), although he did not cite this paper in this connection. These characters—some of them emphasized as early as 1839 by Waterhouse—and others have been reviewed repeatedly (Alston, 1876; Winge, 1887; Tullberg, 1899; Landry, 1957; Lavocat, 1974b, 1976; Wood, 1974a, 1975a; Hoffstetter, 1975—to give only a partial list). We regret the necessity of again going over this ground.

Lavocat's 16 characters are discussed below, in a somewhat different order than that in which he listed them; the italicized statements heading each section are his identifications of the characters, in translation. We have added a few

other characters that he did not mention. In the course of our comparisons we have examined approximately 1000 skulls representing nearly all Recent hystricognath genera, mostly from the Museum of Comparative Zoology.

Lavocat (1971a) went into some detail as to structural similarities between the caviomorphs and the Old World hystricognaths, which he felt were too great (*op. cit.*: 521) to have developed as parallelisms. He stated that the occurrence of the same features in sciurognathous forms does not prove relationship. This is the problem that faces the student of rodents—when are identical structures proof of close relationship, and when does identity merely indicate parallelism? We have tried to find data supporting or contradicting Lavocat's statements. The necessity of providing documentation for our disagreement with some of his conclusions has considerably lengthened this section of our paper.

(2) *Hystricognath mandible.* This is the basic character of the Suborder Hystricognathi, and the only feature known to us that is universally present in hystricognaths and never present in sciurognaths. Hoffstetter (1973: 159, 161) seemed willing to accept the multiple origin of hystricognathy, not believing that *Prolapsus* or *Tsaganomys* had anything to do with the Hystricognathi. He eliminated *Tsaganomys* from the Hystricognathi because it was not hystricomorphous, but apparently was willing to accept the equally non-hystricomorphous bathyergids as members of the Hystricognathi. It is possible that hystricognathy evolved more than once in the course of rodent evolution, but we believe that acceptance of such an occurrence would mean that there are no morphological features (and probably no non-morphological ones) that can be used in establishing subordinal divisions of the Order Rodentia, since all other structures have already been shown to have evolved independently, in various groups of rodents, by parallelism (Wood, 1975a: Fig. 1). Furthermore, if hystricognathy can be assumed to have developed more than once among rodents as parallelisms, we believe that there is no justification whatever for assuming special relationship between the Caviomorpha and the Old World hystricognaths. We prefer to accept, as a working hypothesis, the postulate that hystricognathy originated only once, in the late Paleocene, probably of North America, and that it began as the condition that Wood has variously referred to as "incipiently hystricognath" (1962a: 117, 122; 1974b: 31, 42–43; 1977b: 104; 1981: 81, 82), "hystricognath condition" (1962a: 142), or "subhystricognathous" (1975a: 79; 1981: 86), rather than springing into existence full-blown, like Athena (Wood, 1980c: 270). We therefore include in the suborder all forms that are subhystricognathous or hystricognathous, believing them to have been derived from late Paleocene franimorphs such as *Franimys*. Since some franimorphs were fully hystricognathous (Wood, 1972: Fig. 1; 1974b: Fig. 5), inheritance from a common ancestor is, at the very least, as plausible a hypothesis to explain the possession of such mandibles by the Caviomorpha and the Old World hystricognaths as is one postulating a direct thryonomyoid-caviomorph relationship.

One of the major changes that developed among rodents in general during the Eocene was the increase in gnawing ability. This involved a number of structural changes: the forward growth of parts of the masseter, increasing the length of that muscle for more efficient gnawing (Wood, 1965: 116–119; Lavocat, 1971a: 519); in some forms, the lengthening of the *M. pterygoideus internus*, which served the same function as the lengthening of the masseter; and the modification of the histology of the incisor enamel, increasing its strength (Wilson, 1972: 220–222). One very important point to note here is that these changes did not

occur instantaneously as the result of a single mutation, but built up gradually over considerable periods of time. Nor were they universally correlated with each other, but rather each feature evolved independently. Any slight shift in any one of these features would have been selectively advantageous. All of these changes may be observed taking place among North American Eocene franimorphs.

We do not know whether the Caviomorpha, the Thryonomyoidea, the Bathyergoidea and the Hystricidae developed full hystricognathy independently from subhystricognathous franimorph ancestors, inherited it directly from hystricognathous franimorphs, or whether the Old World forms inherited it from a common ancestor later than their common ancestor with the caviomorphs. There is at present no way of choosing among these choices other than following one's personal preferences.

A mandibular feature, not mentioned by Lavocat, that very frequently accompanies hystricognathy, although neither universally nor exclusively, is a projection extending posteriorly behind and below the condyle. This, the post-condyloid process of Woods (1972: Fig. 1A), varies in degree of prominence from absent (or at least scarcely defined) in, e.g., bathyergids, *Octodon*, *Echimys* and *Trichys*, to large in, e.g., *Kannabateomys*, *Dasyprocta*, *Dinomys* and *Hydrochoerus*, among living forms. It is slightly to moderately developed in Santacruzian caviomorphs and large in the East African *Paraphiomys*, but small in *Petromus* and *Thryonomys*. *Platypittamys* possesses a very small post-condyloid process, *Incamys* one of moderate size. Within the Franimorpha, this area has so far been described only in two species of *Reithroparamys*. The process is lacking in *R. delicatissimus*, incipient in *R. huerfanensis* (Wood, 1962a: Figs. 41D, 46F).

The degree of prominence of the post-condyloid process—indeed its very existence—is dependent on the size, and hence importance in the chewing function, of two masticatory muscles. These are *M. masseter lateralis profundus, pars posterior*, deep division, whose fibers insert on the lateral surface of the ascending ramus and on the posterior margin of the post-condyloid process; and *M. pterygoideus externus*, which inserts below the condyle and on the medial face of the process (Woods, 1972: 127–128, 130–131). Dependence of the process on the muscles is neatly demonstrated by *Ctenomys*, "in which the pterygoideus externus is somewhat small, the expansion has moved laterally and exists as a tubercle" (Woods, 1972: 131) below and lateral to the condyle (Ellerman, 1940: Fig. 38) for insertion of the deep division of the *M. masseter lateralis*. The very frequent association of the process with hystricognathy is, we suspect, because the development of the process has permitted the anteroposterior lengthening of the *M. masseter lateralis profundus, pars posterior*, deep division, and of the *M. pterygoideus externus*, serving the same function as the similar lengthening of *M. pterygoideus internus*, that produced hystricognathy. We suspect that the process arose independently in the Old and New Worlds, although it is possibly present in some franimorphs other than *Reithroparamys huerfanensis*, and may or may not have been present in the numerous franimorphs in which this area has not been preserved.

Although not strictly relevant to the question at issue, another direct consequence of hystricognathy or sciurognathy deserves mention. This is the course taken by the lower incisor in those forms in which the tooth has lengthened posteriorly. Since the axis in the posterior portion of this tooth in rodents is aligned dorsolaterally, the elongating base in hystricognaths can only terminate beneath the condyle, which is situated above it. In those sciurognathous forms in which elongation occurs, the base of

the incisor can only extend upward lateral to the condyle, which is situated medial to the axis. The result is that, depending on the extent of elongation achieved, the base forms a protuberance on the outer side of the ascending ramus, ranging from small and low to so large as to reach the level of the condyle.

(3) *Pterygoid fossa opens anteriorly into the orbitotemporal fossa.* The pterygoid fossa of hystricognaths is bounded by the alisphenoid laterally, the palatine ventrally, anteriorly, and medially, and by the pterygoid posterolaterally; degrees of participation of these elements are highly variable, as are the size and shape of the fossa. "The main trends . . . are toward elongation of the internal pterygoid and horizontal positioning of the muscle. These trends [result from] the movement of the origin of the muscle deep into the pterygoid fossa, and the movement of the insertion to the tip of the extended and laterally displaced angle" (Woods, 1972: 131).

The opening into the orbito-temporal fossa is present in all Recent hystricognaths except *Hydrochoerus*, in which it has been secondarily blocked by the rearward extension of M^3. The opening is a feature much easier to detect in living than in fossil specimens. It is present in all early Miocene Santacruzian caviomorph skulls in which the area is adequately preserved; Scott (1905: 394) doubted its occurrence in *Neoreomys*, but we have found it to be present at the bottom of a deep and very narrow pterygoid fossa. An opening definitely occurs in the East African early Miocene *Paraphiomys pigotti* and *Bathyergoides neotertiarius* (Lavocat, 1973: Pl. 24, Figs. 3, 4; Pl. 7, Figs. 1, 5), and we assume one to have been present in other contemporary African hystricognaths, although Lavocat's figures do not show the opening in *Paraphiomys stromeri* (Lavocat, 1973: Pl. 24, Fig. 1) or *Diamantomys luederitzi* (Lavocat, 1973: Pl. 24, Fig. 2). The character is fully developed in *Tsaganomys*. The skull is not known for any Fayum thryonomyoid, but we suspect that their pterygoid fossa opened into the orbito-temporal fossa.

Among the few known Deseadan caviomorph skulls, only one specimen is sufficiently complete and adequately enough prepared to reveal details of the pterygoid region. This is PU no. 21945, *Incamys bolivianus* (p. 409). Here, connection with the orbit is definitely present. The character was probably present in all Deseadan caviomorphs.

In the three described early franimorph skulls, those of *Franimys*, *Reithroparamys* and *Protoptychus*, this area is either damaged or missing. Wahlert (1973: 8) remarked, of *Protoptychus*, that the fossa ". . . is very deep, and inadequately preserved for full description." The breakage in all of these skulls may have occurred because the area was weakened by perforation of the fossa, but there can be no certainty on this point at present.

With the opening of the dorsal side of the fossa, the origin of the *M. pterygoideus internus* passes forward mediad of a bridge of bone of varying length, the alisphenoid bridge of Woods (1972: 130). The bridge is formed in large part by the alisphenoid, dorsally, and to a much lesser extent by the pterygoid, ventrally. Woods reported the bridge as lacking in *Erethizon*. However, a large series of specimens in the MCZ reveals the bridge to be highly variable, ranging from present, but small and delicate, to interrupted in the center, to absent with no separate alisphenoid canal. Reduction is certainly secondary. A specimen of *Echinoprocta* shows a well-developed bridge and canal. Within a series of *Coendou*, variation extends from a well-developed bridge with a canal, to a delicate one without a canal.

The area of origin of *M. pterygoideus internus* extends forward to the vicinity of the sphenopalatine foramen, in various forms lying in a conspicuous channel in

the adjacent bone. As the muscle enlarged, its passage encroached upon the alisphenoid canal. In some forms passage and canal are separated by a delicate bar of bone within the passage; in others a small projection remains to mark the former position of the separation; in yet others all trace of a division has been lost. In extreme cases, as in bathyergids, the origin of the muscle extends, via an opening, into the brain case as well. Where this occurs, the basisphenoid and the posterior portion of the presphenoid rise steeply to their dorsal midline, and form a narrow ridge flanked by depressions for the origin of the muscles.

Deepening and, ultimately, perforation of the fossa is a character definitely, although not exclusively, associated with hystricognathy. As is well known, it occurs elsewhere in the order among geomyoids and in *Spalax*; it is also present in *Aplodontia,* in which the perforation is large. Anterior to it and lateral to the sphenopalatine foramen in *Aplodontia* is a shallow but clearly defined channel as in various hystricognaths. We have not had the opportunity to dissect preserved material, but in a series of skulls we have detected dried muscle fibers within the passage and attaching to the channel leading forward from it, presumably indicating that it carried *M. pterygoideus internus.* The perforation in *Aplodontia* has usually been considered, as by Wahlert (1974b: 404), to be a very large alisphenoid canal. The internal maxillary artery and vein no doubt pass through together with the muscle, but, again as in various hystricognaths, no trace of a bony separation remains.

In all forms with a perforated pterygoid fossa, the angular region of the mandible, either the whole, as in hystricognaths, or the posterior part, as in the sciurognathous forms, is everted. The presence of a perforated pterygoid fossa in some sciurognaths adequately demonstrates, we believe, that this structure was capable of evolving independently, as parallelisms, among rodents. Furthermore, there is no evidence as to whether the perforation of the fossa arose among Eocene franimorphs, or not until the establishment of the modern infraorders.

We believe that hystricognathy began, in the early Reithroparamyidae, as a means of increasing the length of *M. pterygoideus internus,* because of its importance to the functioning of the lower incisors. At this stage, even very slight and incipient hystricognathy would have been of selective value and hence preserved. Selection for increasing incisor usage would have resulted in lengthening the internal pterygoid, which could have taken place either by moving the origin of the muscle (deepening the fossa), or moving its insertion (developing hystricognathy), or both. We believe that these two features (hystricognathy and deepening of the pterygoid fossa) evolved together, as secondary results of the muscle elongation (Lavocat, 1971a: 519; Woods, 1972: 131; Wood, 1980c: 269–270).

(4) *Inferior border of the zygomatic arch very often bearing an elevated vertical blade for the origin of the masseter.* What Lavocat refers to here, at least in part, is evidently the zygomatic masseteric fossa of Landry (1957: Fig. 11), the jugal fossa of Woods (1972: Fig. 1). This depression, when present, serves, together with the ventral margin of the posterior part of the malar, as the area of origin of *M. masseter lateralis profundus, pars posterior,* deep division (Woods, 1972: 127–128).

Among Eocene rodents, there is a well-developed jugal fossa in *Reithroparamys delicatissimus,* the only franimorph for which the zygomatic arch has been described (Wood, 1962a: Fig. 41C). A fossa is also present in *Paramys delicatus* and *P. copei* (Wood, 1962a: Figs. 2B, 13B), *Ischyrotomus horribilis* and *I. oweni* (*op. cit.*: Figs. 68C, 71C), and *Sciuravus nitidus* (Dawson, 1961: Pl. 5). The jugal fossa is poorly developed to nonexistent

in *Thisbemys corrugatus* (Wood, 1962a: Fig. 36A), the only other Eocene rodent in which this area has been figured. It would thus seem that presence of a jugal fossa is a primitive rodent character.

In hystricognaths, the character is an extremely variable one. Among living Old World hystricognaths, the fossa is absent in the Bathyergidae and weakly, if at all, developed in the Hystricidae. Woods (1972: 127) stated that the fossa is absent in *Thryonomys* but present in *Petromus*, although no part of the muscle takes origin from it. We were unable to identify a jugal fossa in *Petromus*, but found that both genera have a more anteriorly situated depression in the lateral side of the zygomatic arch. This lies mainly in the maxilla, which in these forms extends farther back in the ventral portion of the arch than is generally the case in other hystricognaths (Ellerman, 1940: Figs. 26–27, 29–30). This anterior depression is larger in *Thryonomys*, but other than that we can detect no difference between the two forms, and consider both as lacking a jugal fossa in the strict sense. Lavocat (1973: 168) and Woods (1972: 127) apparently both equated the anterior depression of *Petromus* with the true jugal fossa, thus lumping two different bone-muscle relationships as one supposed character.

Among caviomorphs, the jugal fossa is absent or virtually so in the Erethizontidae, Chinchilloidea and Cavioidea, being essentially limited to the Octodontoidea. Even within this superfamily it varies from absent to large in the Octodontidae and from small to large in the Echimyidae.

The East African Miocene *Paraphiomys* and *Diamantomys* in general resemble *Petromus* and *Thryonomys*, with the exception that the more anterior (not the jugal) fossa presents more ventrally. Such Santacruzian erethizontid, cavioid and chinchillid specimens as are sufficiently well preserved to show this region lack the jugal fossa, as does the Deseadan cavioid *Incamys*. Of fossil octodontoids, the Santacruzian echimyid *Acarechimys minutus* (see Appendix 2) has a small fossa (Scott, 1905: Pl. 67, Fig. 10b) while the Deseadan octodontid *Platypittamys* shows no trace of one.

Since the jugal fossa serves as part of the area of origin of the deep division of *M. masseter lateralis, pars posterior*, and the post-condyloid process of the mandible as part of the area of its insertion, one might expect a fair degree of correlation between the two. This is definitely not the case, however. The process varies from small to large in those caviomorph superfamilies in which the fossa is essentially lacking, while within the Octodontoidea every change is rung from absence of both, to small size of one and large size of the other, to large size of both.

Presence of a jugal fossa is, therefore, not of any significance at higher taxonomic levels, and is, in any case, apparently a primitive rodent characteristic. The myological character associated with it, the high degree of differentiation of the deep from the superficial division of *M. masseter lateralis, pars posterior*, is significant. It occurs in all living hystricognaths that have been investigated in sufficient detail to reveal it. There is some evidence that the division of this muscle may be associated not only with hystricognathy, but also with hystricomorphy, since the hystricomorphous but sciurognathous ctenodactylids possess a well-defined jugal fossa. Whether or not this is accompanied by any marked degree of differentiation of the deep from the superficial division of *M. masseter lateralis, pars posterior*, apparently is not known.

These data indicate that the presence of a jugal fossa is not a hystricognath character; it could have been independently inherited from Eocene franimorph ancestors in those forms where it is present; or it could have been secondarily reacquired independently in the octodontoids and hystricids.

It should be pointed out that modification of the masseter complex began

very early in rodent history, as indicated not only by the hystricomorphous franimorphs but also by the large jugal fossa borne on a descending flange, which extends over the entire length of the malar in the Bridgeran manitshine paramyid *Ischyrotomus horribilis* (Wood, 1962a: Fig. 68C).

(5) *In both, the infraorbital foramen is of the hystricomorphous type.* This is indeed a resemblance between the New and some of the Old World members of the suborder, involving, as it does, the same structural modifications and forward migration of the origin of *M. masseter medialis,* but it is not universal within the suborder—the protrogomorphous Tsaganomyidae and Bathyergidae (p. 517) lack it, and the foramen is very small for a hystricognath in *Platypittamys* (Wood, 1949: Fig. 2; 1974b: Fig. 3A). Nor, as is very well known, is this condition confined to the Hystricognathi. It occurs in the European Eocene to Oligocene Theridomyoidea; the Asian, African and European Ctenodactylidae; the African Anomaluridae and Pedetidae; the Eurasian, North American and African Dipodoidea; and the African glirid *Graphiurus*—all sciurognathous forms. *Prototoptychus*, *Prolapsus* and, very possibly, *Rapamys* (Wood, 1962a: 148, Fig. 52A) show that hystricomorphy was early acquired by North American franimorphs. We suspect that it may have developed independently among Asian hystricognaths descended from protrogomorphous franimorphs, and that the fossorial bathyergoids are descended from franimorphs in which hystricomorphy had not become established. As has been demonstrated several times (Wood, 1974b: 38–41; 1975a: 75–77; 1977a: 133–136; 1981: 82), hystricomorphy evolved independently a considerable number of times—perhaps as many as ten or twelve—and cannot be considered proof of relationship, except insofar as parallelism indicates some relationship.

(6) *The malar heavy in front, with a sinuous suture with the maxillary.* Sinuosity of the suture does not necessarily accompany heaviness of the malar, and both features are extremely varied among the Hystricognathi. The bathyergids display neither. In hystricids, the suture varies from simple to slightly sinuous, and the malar may be either heavy (*Atherurus*, *Hystrix*), moderately heavy (*Thecurus*), or comparatively slender (*Trichys*). *Thryonomys* has a very heavy malar and a moderately to highly sinuous suture, *Petromus* one that is but little expanded with only a slightly sinuous suture. Among living caviomorphs, heaviness ranges from extreme (e.g., *Chaetomys*) to nonexistent (e.g., *Echimys*), and sinuosity of the suture, as, e.g., in *Dinomys*, *Myocastor* and *Spalacopus* (which has a slender malar) is the exception, not the rule.

The East African *Paraphiomys* (Lavocat, 1973: Figs. 2A, 3A) and *Diamantomys* (Lavocat, 1973: Fig. 4A,B) possess malars ranging from moderately slender, anteriorly, in *P. stromeri* and *P. pigotti,* to heavy, and the suture resembles that of *Petromus.* It is not preserved in any other described Oligocene or Miocene thryonomyoid.

The Santacruzian caviomorphs, like their living relatives, display variability as regards both features. Only in *Incamys* among early Oligocene hystricognaths is any part of this region preserved (Fig. 12), and here the suture, although irregular, could hardly be described as sinuous. The drawing of the skull of *Sallamys* given by Lavocat (1976: Fig. 1) shows the zygoma fairly well preserved, but with a straight suture. His stereophotograph (1976: Pl. 1, Fig. 4) seems to show about the same thing, except that only the dorsal and ventral roots of the zygoma are present. The only franimorph whose arch area is known is *Reithroparamys delicatissimus*, in which the malar is slender and the suture is not sinuous (Wood, 1962a: Fig. 41C). There is thus no evidence for (but only a little against) a sinuous suture in the early members of

either the Caviomorpha or the Old World hystricognaths.

Among those rodents that are hystricomorphous sciurognaths, variation in anterior heaviness of the malar is also encountered, to an extent equal to that in hystricognaths. The heaviness ranges from nonexistent, as in anomalurids, through moderate, as in such zapodids as *Sicista*, to very great, as in *Pedetes*. This heaviness is almost never present in sciuromorphous or myomorphous rodents, *Castor* being a notable exception. It seems obvious to us that this is a character associated with evolving structural stresses, whose acquisition has been superimposed on a pre-existing hystricomorphous base. Sinuosity of the suture occurs in *Paramys delicatus* (Wood, 1962a: Fig. 2B), but not in other adequately known Eocene rodents.

Anterior heaviness of the malar and sinuosity of its anterior suture seem to us to be worthless as indications of caviomorph-thryonomyoid relationships.

(7) *Middle ear, malleus and incus of the same type. Malleus and incus fused.* The statement regarding the middle ear is apparently based largely on the investigations of Parent, whose work is available to us only in abstract form (Parent, 1976; Lavocat and Parent, 1971). Parent found that hystricognaths possess various middle ear characters in common, which is not surprising, and that thryonomyids, petromurids, hystricids and bathyergids can be distinguished from each other in this region, which is somewhat more surprising. Among the Caviomorpha, he recognized three groups: erethizontids (in which the subordinal characters are "peu marqués"), octodontoids, and cavioids plus chinchillids. Vucetich, however (1975: 486), found features of the middle ear that separate the Chinchillidae from the Cavioidea. Not surprisingly, parallelism crops up in middle ear structure. Certain hystricognath features are met with in *Anomalurus* and *Pedetes*, and *Agouti* ("*Cuniculus*") has a bulla that resembles that of the Hystricidae "de façon inattendue" (Parent, 1976: 244). We can see no evidence in this that caviomorphs were descended from any Old World group; in fact, the situation in erethizontids, as reported by Parent (1976: 244), can be interpreted as ruling out such a relationship. The degrees of differentiation seen within the Old and New World groups are what would be expected, given a rather distant common ancestry.

Knowledge of the middle ear cavity in hystricognaths does not extend farther back in time than the early Miocene (Lavocat, 1973, for *Paraphiomys*; Vucetich, 1975, for *Perimys*). The bulla is unknown in Fayum thryonomyoids, and its dissection has not been practicable in *Incamys*. Among the known Franimorpha, the tympanic is free of the skull only in the very early *Franimys*. Here, the ventral aspect of the periotic, although "difficult to interpret" (Wood, 1962a: 142) is in general similar to that of *Paramys*, as is to be expected. Comparison with most later forms, in which the tympanic surrounds the middle ear cavity, is difficult, being limited in large part to the promontorium. There is a decided difference in the size and shape of this latter structure between the primitive condition exhibited by the early Eocene forms and the more advanced one shown by the Miocene genera that lived some 30 m.y. later. An assessment of this difference must await some knowledge of intermediate stages, but we suspect that, under either hypothesis for the origin of the Caviomorpha, the common ancestors of the living caviomorphs and the Old World hystricognaths were not greatly advanced beyond the paramyid-reithroparamyid level.

Malleus and incus of the same type. As may be seen from the figures and descriptions given by Doran (1879: 413–419, Pl. 60), Tullberg (1899: Pl. 24), Cockerell *et al.* (1914: Figs. 117–119) and others, these ossicles are heavily built and more or less in line dorsally. The head of the

malleus is large and elongate, varying from moderately (Bathyergidae) to extremely so (*Chinchilla*); the neck is short, and the lamina small.

Ossicles are frequently absent from within the bullae of fossil mammals. This is not surprising in view of field observations by one of us (B.P.) that fly larvae in the course of their development can pullulate through even the smallest openings in decomposing bodies and are fully capable of dislodging and moving out such small objects as ear ossicles.

Knowledge of the *ossicula auditus* of hystricognaths does not extend farther back than the Miocene. Among fossil hystricognaths only three examples of the malleus and incus have been reported: *Drytomomys aequatorialis* (Fig. 23A–C and Fields, 1957: 343, 347–349; Fig. 23E,F); *Perimys* sp. (Vucetich, 1975: 484, 488); and *Paraphiomys pigotti* (Lavocat, 1973: 34; Pl. 13, Fig. 4; Pl. 40, Fig. 1). All three sets, as might be expected, are of hystricognath type. *Drytomomys* is similar to *Dinomys*, but *Perimys*, a chinchilloid, is closer to *Cavia*, especially in the relative shortness of the head of the malleus, than to the living members of its superfamily. *Paraphiomys* seems to us to be close to *Petromus*; it is certainly very different from the bathyergids, and the head of the malleus is more slender than in *Thryonomys*. There is, as Lavocat noted (1973: 34), a resemblance to that of *Dasyprocta*.

In assessing the ossicular evidence, the same difficulty is encountered as in the case of middle ear structures, namely lack of information, in this case total, regarding pre-Miocene evolutionary stages.

Malleus and incus fused. Fusion of the malleus and incus is not confined to the Hystricognathi, since the Ctenodactylidae show it also, and Doran (1879) reported it as being variably present in *Dipus*. It would seem to be universally present in Old World hystricognaths. It is not a universal feature, however, among the Caviomorpha. Vucetich informs us (personal communication) that, in perhaps 1% of adult *Cavia* whose ossicles she has seen, she was able to separate the malleus and incus without breakage. We have recorded (1959: 292–293) a lack of fusion in some adult specimens of *Octodon*, *Aconaemys*, *Spalacopus* and *Echimys*; and such a lack had earlier been reported in *Proechimys* (Cockerell *et al.*, 1914: 372), and, earlier still, in *Myocastor* (Hyrtl, 1845). There is therefore no justification for the unqualified statement that fusion is universal in the Hystricognathi.

To the above list of non-fused ossicles, we now add a young adult of the late Miocene dinomyid *Drytomomys aequatorialis*. Fields' figures (1957: Fig. 23E,F), while suggesting fusion, showed a very definite groove between the bones. Subsequent to his work, the specimen was badly damaged with accompanying loss of the manubrium mallei and of the incus, the two ossicles parting at the groove. A thin film of matrix extended over the entire articular surface of the malleus separating it from the incus; fusion had not occurred (Fig. 29).

Lavocat reported that the malleus and incus of *Paraphiomys pigotti* were fused, presumably because they were lying within the bulla in an articulated position. His figure (1973: Pl. 13, Fig. 4) suggests that there is a matrix-filled groove at their junction. This raises the possibility that, as in the case of *Drytomomys*, they may have been separable in life. In fact, it would seem to us that, although lack of fusion can be demonstrated in fossil rodents if the ossicles are preserved separately, fusion can only be proven by serial sections or when a continuous groove between the ossicles is no longer present.

Vucetich (1975: 484), although not mentioning fusion, remarked of *Perimys* sp. that the suture between the two ossicles was simple on both sides.

In some, but not all, Old World hystricognaths the area of fusion extends to the

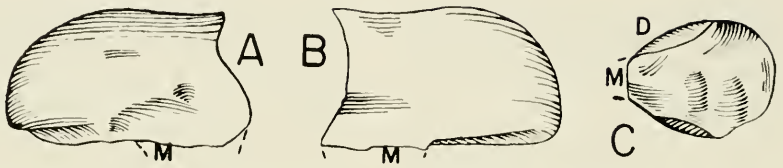

Figure 29. Malleus of *Drytomomys aequatorialis*, UCMP no. 41636, ×15. A. Dorsal view. B. Ventral view. C. Surface for articulation with the incus.

Abbreviations: D—dorsal side; M—broken manubrium.

crus longus of the incus, moderately so in *Thryonomys* (Tullberg, 1899: Pl. 24, Fig. 14; Wood and Patterson, 1959: 293, n. 4), although Doran's figure does not show this, and almost as far as the incudal articulation in bathyergids (Hyrtl, 1845; Doran, 1879: 413; Tullberg, 1899: Pl. 24, Figs. 1–2). *Hystrix* (Doran; Tullberg), *Petromus* (Tullberg and personal observation), and all caviomorphs for which ossicles are known display no such extension. We do not, of course, feel that the similar degree of fusion of the malleus with the crus longus of the incus indicates closer relationships of *Thryonomys* to the bathyergids than to *Petromus*.

Among those hystricognaths—and they constitute the great majority—in which fusion occurs, the time of onset of the fusion during ontogeny is variable. Available data are few but sufficient to demonstrate this. Doran has recorded fusion in newborn *Cavia*, "even in very young" *Dasyprocta*, and in "quite young" *Hystrix*, whereas in *Hydrochoerus* the ossicles are "often free in young" specimens; we have recorded fusion in juvenile *Thryonomys* and in adult, but not in juvenile, *Abrocoma*. Thus the available data suggest that the ontogenetic onset of fusion is earlier in Old World than in New World forms, and all stages from *in utero* fusion to complete lack of fusion may occur in the latter.

There has been no documented selective basis for the fusion of these ossicles. However, Dr. E. C. Oaks has suggested to us (*in lit.*) that it may be an adaptation against possible dislocation of unusually heavy ossicles such as characterize most of the Hystricognathi.

If the Caviomorpha were descended from rafted thryonomyoids, it seems most amazing to us that the more primitive condition (occasional absence of fusion) should be rather widespread among the Caviomorpha, presumably descended from a small founder population, and unknown in the Old World forms. We know of no basis for assuming that there has been a selective advantage for a neotenic retention of embryonic lack of fusion among the Caviomorpha that did not act on the Old World forms. Therefore, we conclude that the status of fusion of the malleus and incus supports one of two possibilities. Either the Old World hystricognaths were descended from caviomorph ancestors; or (much more probably, in our opinion), fusion was either incipiently present among the Franimorpha or was acquired independently, by parallelism, by the Old World and New World hystricognaths, as well as in such unrelated rodents as the sciurognathous ctenodactylids (Wood, 1975a: Fig. 1).

(8) *Similar arrangement of openings at the base of the skull.* We are not sure to what this refers, unless to the foramina for the cranial arteries. In view of the reported similarities in cephalic arterial circulation between the Caviomorpha and the Old World hystricognaths (Guthrie, 1963: 472; Bugge, 1971: 519–522; 1974a: 70–71; 1974b: 65–69), a similarity of the foramina through which the arteries pass is not surprising. Unfortunately, Old World Oligocene material (other than of

tsaganomyids) is unavailable to demonstrate either similarity or dissimilarity to the Deseadan caviomorphs.

Recent studies by Bugge (1971, 1974a, 1974b), Guthrie (1963) and Wahlert (1974a) have provided enough new information on the cranial circulation of rodents so that the arrangement of these blood vessels (or of the foramina presumed to have been occupied by them) can be used as an important adjunct to rodent classification. Bugge (1974a, 1974b) has developed a classification of the rodents, using the losses, during ontogeny, of arteries (especially the stapedial and internal carotid) from the primitive mammalian pattern. He reported (1974b: 78) that the "stapedial artery obliterates when the bulla and pars petrosa are nearly connected and when the chewing musculature is very strongly developed, and I think that there is some mechanical explanation for obliteration of the stapedial artery. But I do not know why the internal carotid artery is obliterated in some cases and not in others." It would seem possible that the same types of processes would have affected the internal carotid as the stapedial artery. If Bugge was correct, that the fusion of the bulla with the skull was responsible for the loss of the stapedial artery, this loss should have occurred among Eocene franimorphs, in some of which the bulla is fully developed and fused with the skull (Wood, 1962a: Fig. 41B,C; Wahlert, 1973: Fig. 2; 1974a: Fig. 5).

As pointed out by Bugge (1974a: 56, Fig. 15B), the arterial pattern of *Coendou prehensilis* is quite different from that of other hystricognaths; it is apparently most similar, among living rodents (other than *Erethizon*, in which, apparently, the cephalic arteries have not been studied, although a carotid canal was reported by Hill in 1935), to that of *Castor fiber* (Bugge, 1974a: Fig. 10C), and seems to be almost identical to what Bugge (1974a: Fig. 15D) described for *Oryctolagus* and *Lepus*. The difference between *Coendou* and the other hystricognaths is so striking that Bugge (1974a: 56) felt that the erection of a new Suborder Erethizontomorpha was needed (Bugge did not use the Suborders Sciurognathi and Hystricognathi that we are using; his suborders are therefore equivalent to our infraorders).

The cranial circulation of the Chinchillidae, Octodontoidea, *Thryonomys* and the Bathyergidae is essentially identical, with the internal carotid, proximal part of the stapedial and varying amounts of the central part of the supraorbital arteries having been lost (Bugge, 1974a: Figs. 14D, 15A). The Hystricidae differ by developing a transient anastomosis (a6) between the distal part of the internal carotid and the infraorbital arteries (Bugge, 1974a: Fig. 15C). Slightly different anastomoses occur in the cavioids, with a transient connection (a4) from the distal internal carotid to the supraorbital in *Dolichotis* (*op. cit.*: Fig. 14B); a transient one (a5″) from the same source to the infraorbital in *Cavia* (*op. cit.*: Fig. 14A); and a permanent connection in approximately the same area (a6) in *Galea* and *Dasyprocta* (*op. cit.*: Fig. 14C).

Problems arise in connection with reliance on the pattern of cranial circulation as a guide to rodent relationships. We do not know of the selective pressures that led to the changes, other than Bugge's suggestion that the loss of the stapedial artery was related to the fusion of the bulla with the skull. As a result, it is difficult to assess the weight to be given such changes. How can one be sure, in dealing with fossils, that an opening in the skull carried the blood vessels that one would anticipate, on the basis of the study of Recent forms? This point is raised by the observation by Wahlert (1974a: 373) that the carotid canal of *Marmota monax* carries the inferior petrosal sinus rather than the internal carotid artery, as is usually the case among rodents. Bugge (1974a: Fig. 11B) indicates the internal carotid artery to be absent in *Mar-*

mota marmota as well. Finally, how does one distinguish parallelism or convergence in the gain or loss of blood vessels from the inheritance of a pattern from a common ancestral source?

The similarities cited above between *Coendou*, *Castor*, and leporids, and the likewise great similarities between *Muscardinus* and *Aplodontia* (Bugge, 1974a: Fig. 13C,D), are certainly not indications of close relationships. The first three have interrupted the stapedial, supraorbital and internal ophthalmic arteries, and have acquired anastomoses a1, a2, and a3′ in the adult as well as a3 transiently during ontogeny (Bugge, 1974a: Figs. 10C; 15B,D). *Muscardinus* and *Aplodontia* have lost the internal carotid, stapedial and supraorbital arteries and have developed the a3 anastomosis; *Aplodontia* has also acquired an a3″ anastomosis. Since none of these forms are at all closely related, the losses and gains must be presumed to have occurred as convergent adaptations. If these similarities are not indicative of relationship, we see no real reason for believing that the similarly close resemblances between the chinchillids, octodontoids, *Thryonomys* and the bathyergids (Bugge, 1974a: Figs. 14D, 15A) could not either be inheritances from a common Eocene franimorph ancestry or the result of parallelism. The fact that three different types of anastomosis occur in the caviids (Bugge, 1974a: Fig. 14A–C) suggests that similarities and differences in the cephalic circulation need to be treated with caution.

The pattern of circulation described in *Coendou* by Bugge (1974a: 56) is certainly much more primitive than that in any other hystricognath that he dissected. As he has indicated (Bugge, 1974b: 78), "these arteries pass through canals in the cephalic bones and when these arteries are [lost, the] canals are also obliterated. Therefore I would think it most unlikely that such osseous canals should re-open for the internal carotid artery or the stapedial artery." If Lavocat is correct that all the caviomorphs (including the Erethizontidae) are descended from thryonomyoids, it is surprising that no trace of the internal carotid has been preserved in any of the Old World hystricognaths that Bugge dissected. However, and this we consider to be an important point, if the caviomorphs (including the Erethizontidae) *are* descended from thryonomyoids, it must follow either that the erethizontids have reacquired the internal carotid artery or that the loss of the internal carotid has occurred independently, as a parallelism, in the Old and New Worlds.

There is some evidence as to the situation in the fossils. Unfortunately, no cranial material is available from Oligocene thryonomyoids. Bugge (1974a: 63) thought that "... it is a reasonable assumption that both the internal carotid artery and the stapedial artery were already obliterated in the Oligocene-Miocene phiomyids ...." Lavocat (1973: 63), however, reported that, in *Diamantomys luederitzi*, "Le foramen carotidien s'ouvre en avant de la gouttière ... qui se creuse entre la région postérieure du basi-occipital et la bulle. C'est un trou de toute la hauteur de la gouttière." As indicated above (p. 411), there is possibly a small carotid canal in *Incamys*. These observations suggest that the internal carotid artery was still present in *Diamantomys* and possibly in *Incamys*, again indicating that the artery has been lost independently in the New and Old Worlds. Incidentally, Wahlert (1974a: Fig. 10) identified a carotid canal in the North American early Oligocene franimorph cylindrodont *Ardynomys occidentalis*.

We feel, in summary, that the cranial circulation very probably indicates that the Caviomorpha and Old World hystricognaths are related, but that almost certainly one of their similarities, the loss of the internal carotid artery, occurred independently in the two hemispheres. How many of the other circulatory similarities are the result of parallelism and

how many were inherited from common franimorph ancestors, we have no way of knowing at present.

(9) *Alisphenoid remaining in a low position.* This is an advanced character, not a primitive one as Lavocat's wording might suggest. In most Eocene rodents, as may be seen in the figures of Wood (1962a; 1974b: Fig. 4B) and Wahlert (1974b), the alisphenoid extends dorsally to or above the posterior root of the zygoma, to meet a descending portion of the parietal, the frontal and squamosal being separated. In nearly all later rodents, a reshuffling of relationships between these bones has taken place. The descending portion of the parietal was quickly lost and a squamoso-frontal contact was established, its extent largely depending on the degrees of reduction of the anterolateral portion of the parietal and of the dorsal portion of the alisphenoid. The latter may retain the size met with in the primitive rodents (e.g., *Aplodontia*, many sciurids, *Pedetes*) or may increase dorsally until it nearly (e.g., *Tamias, Pteromys*) or quite reaches the parietal (e.g., various sciurids, *Castor*).

In the other direction, the dorsal portion of the alisphenoid may be reduced to varying degrees until it comes to lie ventral to the level of the root of the zygoma or to that of the glenoid cavity. This occurs in many muroids as well as in the Hystricognathi. Within the latter, as Landry (1957, Table 2) has noted, the bathyergids do not display quite the same degree of reduction as do the others. *Incamys*, the only early Oligocene hystricognath in which this portion of the skull is known, has a low alisphenoid that extends no higher than the root of the zygoma (Figs. 12, 15A). In the Eocene *Protoptychus* the critical area is obscured, but from what is visible it would seem probable that squamosal-frontal contact had become established (Wahlert, 1973: Fig. 2). There is at present no real evidence as to whether alisphenoid reduction took place independently in the surviving hystricognath infraorders or whether the reduction represents inheritance from a common franimorph ancestor. In any event, on the basis of our present knowledge, this character can be considered no more a support for derivation of the Caviomorpha from the Thryonomyoidea than for independent derivation of the two from the Franimorpha.

(10) *Same type of squamosal-mastoid-parietal-occipital junction.* We believe that this statement refers to the presence of a lateral strip of the supraoccipital that extends downward, separating the squamosal from the mastoid process (Lavocat, 1971a: 520). It is present, but does not project freely, in all living Old World hystricognaths, being very large in bathyergids; a small blunt terminal enlargement in an old individual of *Thryonomys* is the closest approach we have seen in thryonomyoids to the projection that occurs in some caviomorphs.

In living caviomorphs, the strip is lacking entirely in the Hydrochoeridae, Dasyproctidae, Dinomyidae and Cuniculidae, and is variable in the Caviidae, being absent in *Cavia*, *Galea* and *Dolichotis*, present in *Microcavia*, and intermediate in *Kerodon*. In most echimyids it projects as a small blunt nubbin, as a blunt projection in capromyines, and culminates in the very long, independent processes of *Myocastor* and *Elasmodontomys*. Among the remaining caviomorphs, it is limited to an enclosed strip of bone. Landry pointed out that the lateral process also occurs in various sciurognathous rodent groups, "and seems . . . to be a more or less random feature among rodents" (1957: 8). It was not present in *Reithroparamys* or *Protoptychus*. *Platypittamys* appears to lack it, and it is small in *Incamys* (Fig. 12). The area is preserved in no other Oligocene hystricognaths.

It seems highly probable to us that this feature evolved independently in the Old and New World hystricognaths; cer-

tainly there is no present evidence that it did not.

(11) *Frequently, elongate cleft between auditory bulla and squamosal.* This character is highly variable. The vacuity seems usually to develop from the vicinity of what Wahlert (1974b: 374) called the post-alar fissure, a foramen or foramina on or near the squamoso-tympanic junction anteriorly; he believed that it transmits a vein tributary to the jugular sinus system. All stages from absence, through a small foramen, to a complete cleft can be seen among living Old World hystricognaths, and the caviomorphs as a whole are just as varied. The cleft does not occur in *Incamys*, *Reithroparamys* or *Protoptychus*. Among other rodents, it seems to be frequent among the Muroidea. We suspect that the varying degrees of development are related to differing stresses in the skull bones, and that this feature has no significance at higher taxonomic levels.

(12) *Maxillary reaches the rear of the floor of the orbito-temporal fossa.* We find this a rather vague characterization, and are not sure what Lavocat was trying to say. We believe that he was referring to this feature earlier on the same page (1973: 168) when he stated that "Nous avons récemment montré (Lavocat, 1972) que les relations du maxillaire et du palatin dans la région du plancher de la cavité orbitaire sont comparables." Unfortunately, he does not include the 1972 paper in his list of references, and we have been unable to locate it. We suspect that this was a reference to Lavocat, 1971b, which he likewise does not cite, but which does discuss this area of *Paramys delicatus*. It is difficult to be sure just what he meant, especially when he stated (Lavocat, 1971b: 119) that Wood (1962a) "ne montre en effet aucune suture séparant le palatin du maxillaire au niveau du trou sphénopalatin." It would seem quite clear to us that Wood (1962a: Fig. 3A) does show a suture separating the palatine from the maxillary in this area, and he specifically stated (1962a: 14) that "The maxillo-palatine and maxillo-orbitosphenoid sutures run behind the rather large sphenopalatine foramen . . . ." Later on the same page, he stated "Within the orbit, all specimens, except the type of *P. copei*, are broken so that the suture between the palatine and the orbitosphenoid cannot be located. In [that] form, however, it can be seen to run from the posterior tip of the maxillary posterodorsally into the foramen lacerum anterius." In *Ischyrotomus*, the palatine is fused with the orbitosphenoid, and is clearly separated from the maxillary (which includes the sphenopalatine foramen) by a suture (Wood, 1962a: 189, Fig. 71C). The description that Lavocat gives (1971b: 118) for the situation in *Thryonomys* seems to be almost exactly the same as that in the paramyids.

It would seem, therefore, that what Lavocat was trying to say was that the hystricognaths have retained the primitive rodent condition. This does not seem to be valid evidence of a thryonomyoid ancestry for the caviomorphs.

(13) *Habitual presence of an interparietal.* This bone is no doubt present embryologically in all members of the order. Thereafter it may remain distinct, fuse with the parietals, the supraoccipital or both, again, we suspect, in relation to skull stresses. All stages of fusion, or lack of it, are met with in both caviomorphs and Old World hystricognaths, as well as in all other rodents. A separate bone is present in the adult, among the pertinent fossils, in *Reithroparamys* (Wood, 1962a: Fig. 41A), *Protoptychus* (Wahlert, 1973: Fig. 2), *Paraphiomys* and *Diamantomys* (Lavocat, 1973: Figs. 3C, 4B). There is no trace of a separate element in *Incamys* (Figs. 7, 8) or in any of the Santacruzian genera figured by Scott (1905), but it was clearly distinct in *Platypittamys* (Wood, 1949: Fig. 1). "Habitual presence of an interparietal" is more descriptive of the Muroidea than of hystricognaths. The character has no significance at higher

taxonomic levels. Lavocat (1971a: 520) and Hoffstetter (1975: 512) apparently agreed with us on this point.

(14) *Lacrimal foramen within the orbit and not on the muzzle in front of the zygomatic arch.* Lavocat was correct in his observation: the Old World hystricognaths and caviomorphs share this character, but they also share it with most other rodents, including the Paramyidae, all other protrogomorphs, all the Franimorpha, *Castor*, *Pedetes*, anomalurids, sciuroids, etc. A forward displacement of the foramen occurs in muroids, glirids and dipodids. The intraorbital position was certainly a primitive rodent character retained by, among many others, the Bathyergoidea, Thryonomyoidea, Hystricidae and Caviomorpha.

(15) *Skeleton: same type of tibia in* Platypittamys *and* Paraphiomys. Lavocat described the tibia of *Paraphiomys* (1973: 91–92), but made no comparisons whatsoever with that of *Platypittamys*. We could find no indication in his 1973 paper as to what he meant, but, earlier (Lavocat, 1971a: 521) he had stated that the arching ("cambrure") of the tibia in *Platypittamys* was similar to that in Old World forms. This does not seem to us to be very significant, in which conclusion Hoffstetter (1975: 513) appears to agree with us.

(16) *Same type of brain.* Lavocat (1973) gave no documentation for this statement, and again we are not sure what he intended to imply. Earlier (1971a: 521) he stated that, while most rodents have smooth brains, a large number of caviomorphs have suggestions of fissuration, which are also present in *Thryonomys* and *Paraphiomys*. In his monograph on the East African Miocene rodents, Lavocat described (1973: 36–37) endocasts of *Paraphiomys pigotti*, *P. stromeri* and *Diamantomys luederitzi*, only the first of these being illustrated (1973: Pl. 1, Fig. 3; Pl. 35, Figs. 1, 3, 5, 6), and he made comparisons, among living forms, only with *Thryonomys*, for which he figured a plastic endocast (1973: Pl. 35, Fig. 2). No comparisons were made with the brains or endocasts of any caviomorphs, and there was no discussion of any of the literature. Unfortunately, we found that most of the details that Lavocat described in the text were not recognizable on his plates.

Hoffstetter (1975: 522) thought that there was a particularly marked tendency toward gyrencephaly in the hystricognaths, and that perhaps there was "una tendencia precoz, posiblemente heredada del antecesor común de los Phiomorpha y Caviomorpha." This last statement is very close to our opinion, although perhaps we differ from Hoffstetter as to what was the common ancestor.

A series of papers by Pilleri (1959a–1959j; 1960a–1960f; 1961a, 1961b; 1962) indicate that, in general, brains of sciuromorphous rodents are more advanced in gyrencephaly than those of myomorphous ones and less advanced than those of hystricognaths. The distinctions among them seem to be largely ones of degree. These degrees of complexity are, again in general, in agreement with the individual size attained by members of these groups, sciuromorphous rodents being on the average larger than myomorphous ones and smaller than hystricognaths. The Muroidea, currently the most successful and widely distributed of the major rodent groups, have brains, so far as known, with smooth neopallia. Study of rodent brains began with those of murids and sciurids, and the impression that rodent brains were all of simple type became established early. *Hydrochoerus* was noted as an exception to the general rule by Dareste (1855). Subsequently, Beddard (1892) described or mentioned the brains of a number of larger rodents in which there were cerebral convolutions.

Landry (1957: 20–22) considered that, among rodents, cerebral convolutions are positively associated with increased size, but are probably more often present in

hystricognathous forms than in sciurognaths of corresponding size. Pilleri (1959b: 77) pointed out that with decrease in relative brain size (approximately the equivalent of increase in body size) the gyrencephaly progressively increases, but that the cane rat *Choeromys* (=*Thryonomys*) *harrisoni* is an exception, being less convoluted than would be expected on the basis of its relative brain size.

Pilleri's illustrations show convolutions to be present in: *Marmota* (1959a: Fig. 8), *Castor* (1959a: Fig. 10; 1959e; 1959i; 1959j), to a slight degree in *Aplodontia* (1960a: Fig. 16), *Sciurus niger* (1960b: Fig. 1), slightly in *Citellus* (1960b: Fig. 5), and in all hystricognaths that he studied (except *Heterocephalus* and *Petromus*), namely *Hystrix*, *Atherurus*, *Cavia*, *Dolichotis*, *Lagostomus*, *Chinchilla*, *Myocastor* and *Choeromys* (=*Thryonomys*) (1959b, 1959d), *Myoprocta*, *Dasyprocta* (1959f, 1959g, 1959h), and *Paradolichotis*, although that form, included by some in *Dolichotis*, is less convoluted than *Dolichotis* (1959g). The only possible exception that he found was *Erethizon* (1959b: 53), although the brains of this form that he illustrated the following year (1960e: Fig. 1) look convoluted. He stated, however, that the brain was smooth (1960e: 370). The brain of *Heterocephalus*, in contrast to those of most genera just discussed, is smooth; resemblances to the brain of *Geomys* were pointed out by Hill *et al.* (1957: 503) and to that of *Aplodontia* by Pilleri (1960a: 30–31). The *Heterocephalus* brain (the only bathyergid described by Pilleri) seems quite different from those of all other hystricognaths so far studied, and impressed Pilleri (1960f) as being very primitive. Later, Pilleri (1962: 494) indicated that the brain of *Petromus* was much more primitive than the brains of the caviomorphs that he had studied, and that *Petromus* and *Thryonomys* "haben sich frühzeitig von den *Ischyromyiden* getrennt und sind heute unter Bewahrung dieser primitiven hirnmorphologischen Merkmalen nur auf den afrikanischen Kontinent beschränkt."

Pilleri (1962: 494) also stated that there was a striking resemblance between the asulcate brain of *Petromus typicus* and that of the ctenodactylid *Pectinator specki* (1962: 494), that "*Pectinator* und *Petromus* stammesgeschichtlich gemeinsame Wurzeln haben" (1962: 495), and that "the brain of *Pedetes caffer* ... shows unmistakable relationships to the Hystricomorpha" (1960d: 382). Since both *Pectinator* and *Pedetes* are sciurognaths, either brain structure is not always a good guide to rodent relationships, or the structure of the angular process of the mandible is not. Dräseke (1929: Fig. 3), however, illustrated a brain of *Pedetes* with an incomplete sulcus lateralis on each hemisphere. It looks as much like that of *Castor* as like most of the hystricognath brains figured by Pilleri.

An interesting point is suggested by the data so far available. No clear evidence of neopallial fissuration is met with in rodents with a head and body length (hbl) of less than about 350 mm, at which size a rudiment of the parasagittal (or longitudinal) fissure may appear. Very few sciuromorphous and even fewer myomorphous rodents attain a hbl of 350 mm or more. The largest sciurid whose brain is known, *Marmota flaviventris* (hbl 470–700), has a depression (Grübchen) running lengthwise that is the homolog of the sulcus lateralis (Pilleri, 1960b: 60). In *Castor* (hbl 735–1300), there is a sulcus lateralis that may be either a simple groove 15–22 mm long (about 30–45% the length of the cerebrum), or it may be subdivided into two or three parts by short breaks in its course (Pilleri, 1959c: 103, 1959e: Fig. 2). Likewise, the largest myomorphous rodent whose brain is known, *Hypogeomys* (hbl to 350), has a short sulcus lateralis and is, as a whole, "rather highly differentiated for a member of the ... Myomorpha" (Pilleri, 1961a: 430).

Greater fissural complication frequent-

ly accompanies increase in size. The only possible exception known to us may be *Octodon* (hbl 125–195). Beddard (1892: 609) stated that the brain of this animal possesses a parasagittal (longitudinal) fissure, but gave neither a figure nor further description. Since other parts of his work do not agree entirely with reports of later investigators—Dräseke (1942) for *Capromys* and *Coendou* and Pilleri (1959b: 60; 1959f; 1959g; 1959h) for *Dasyprocta* and *Cuniculus*, who found certain neopallia to be simpler than indicated by Beddard—we believe that Beddard's report on *Octodon* requires confirmation.

Endocasts, so far as we are aware, have never been described for fossil caviomorphs, so fossil and Recent Old World hystricognath brains can only be compared with those of Recent New World genera. The endocast of *Paraphiomys* (Lavocat, 1973: 36–37; Pl. 1, Fig. 3; Pl. 35, Figs. 1, 3, 5, 6) does not look much like that which he figured for *Thryonomys* (Lavocat, 1973: Pl. 35, Fig. 2), but is closely similar to the actual brains of *Choeromys* (=*Thryonomys*) *harrisoni* (Pilleri, 1959b: Fig. 12) and of *Anomalurus pusillus* (Pilleri, 1959a: Fig. 14). The endocast of *Paraphiomys* is also similar to that of *Pseudocylindrodon texanus* (Wood, 1974a: Fig. 16), an Oligocene franimorph.

In general, we conclude that: (1) the brains of large rodents tend to be more convoluted that those of small ones; (2) the brains of hystricognaths are apt to be somewhat more convoluted than those of sciurognaths of the same size; and (3) at the present time our knowledge of brain form in rodents and its taxonomic value leaves much to be desired. As a caveat, we note that Pilleri (1960e: 375) reported that study of six brains of *Erethizon dorsatum dorsatum* from two localities in Michigan showed great variability in the form of the cerebral hemispheres. He also considered that the similarity of the brains of *Heterocephalus* and *Aplodontia*, together with the presence in each genus of two superior venae cavae, suggests a phylogenetic relationship (Pilleri, 1960a: 34—summary), a suggestion that will not appeal to many students of the order.

(17) *Same type of upper and lower molars in the Deseadan* Eosteiromys *and the Phiomyidae. Same type of primitive premolar in certain Fayum phiomyids and certain Deseadan caviomorphs.* We assume that Lavocat's use of the Colhuehuapian *Eosteiromys* was a *lapsus calami* for the Deseadan *Protosteiromys*. The following discussion, however, applies whichever genus he meant. For the terminology that we use for the parts of the cheek teeth, see Figs. 1–2, pp. 376–377).

General. The most detailed argument for close dental similarity between the Caviomorpha and Old World hystricognaths was made by Stehlin and Schaub (1951), who based their entire philosophy of rodent interrelationships, as spelled out later by Schaub (1953a, 1953b, 1958) on the supposedly fundamental importance of a tooth pattern consisting of five transverse crests in the upper molars (the "*Theridomys-Trechomysplan*"), the fifth crest (the mesoloph, the last of the five to evolve) occurring in the center of the tooth, as in the upper teeth of *Phiomys* and *Metaphiomys* (Fig. 30C,D,F). This pattern is exceedingly common among rodents and is a dental adaptation that occurred independently many times throughout the order (e.g., Theridomyoidea, Eomyidae, Cricetidae if not derived from eomyids, Dipodoidea, Castorimorpha, Anomaluridae, and whatever number of hystricognaths developed it independently). This pattern, we believe, is an adaptation to the need for an increased chewing area in animals that had reduced the cheek teeth at least to P_1^{2-1}, M_3^3 before a shift to the consumption of harsh food led to strong selective pressures for more efficient grinding surfaces. If this is correct, it should come as no surprise to anyone familiar with rodent evolution that a superficially similar and functionally identical tooth pattern should have evolved in both the

Caviomorpha and Old World hystricognaths as a reaction to the same selective pressures. This, in itself, cannot be taken as evidence of relationship below the ordinal level.

We have argued in detail (1959: 407–412) against the postulate that the "*Theridomys-Trechomysplan*" had the basic importance that Schaub believed, and we see no need to repeat all our arguments, since we feel that no evidence has been brought to bear against them. Lavocat's argument for a dental identity of early caviomorphs and thryonomyoids arises, we believe, from an acceptance of a common ancestral five-crested pattern as the basis for much of rodent dental evolution. Such a point of view (due in our opinion to a mistaken belief that the pentalophodont Theridomyoidea, so important in the European Eocene and Oligocene, could not have died out without issue) has often been implicit in work on rodent evolution by European students since the days of Schlosser, who considered (1884b: 102–105) that the theridomyoids were not only ancestral to the Hystricidae and Caviomorpha, but also (likewise on the basis of equal similarities of the tooth structure) to the Castoridae. Lavocat, not citing Schlosser's earlier work, stated (1976: 84) that "Frappé de son côté des resemblances dentaires également très étroits, Schlosser (1911) avait proposé l'hypothèse d'une origine Theridomyidae du genre *Phiomys* de l'Oligocène du Fayoum" (as indicated by Wood, 1968: 34, the specimens figured by Schlosser, that he referred to *Phiomys*, were actually *Metaphiomys schaubi* and *Gaudeamus aegyptius*).

Schaub's Pentalophodonta (1953a) has much in common with a phylogenetic tree offered more than half a century earlier by Schlosser (1884a: 327); the "*Theridomys-Trechomysplan*" of Stehlin and Schaub (1951) could be said to be merely an expansion and up-date of this diagram. As recently as 1971, Lavocat (1971a: 518) believed that there were too many differences between the thryonomyoids and the theridomyoids (such as that the latter were sciurognathous) for anyone to admit a close relationship between the two. However, later (Lavocat, 1976: 84–86) he has returned at least part way toward the Schlosserian view point in his advocacy—mistaken in our opinion—of a relationship at some stage between the Thryonomyoidea and the sciurognathous Theridomyoidea. Lavocat, however, apparently does not follow Schlosser (1884b: 102–105) in deriving the Castoridae from the Theridomyoidea.

In contrast to Schlosser and Lavocat, Stromer, the first student of significant quantities of Miocene African rodents, questioned relationships between thryonomyoids and caviomorphs. "Die mir vorliegenden Reste lassen sich, soweit vorläufig bestimmbar, fast alle mit *Hystricomorpha* im weitesten Sinne am besten vergleichen, scheinen jedoch bemerkenswerter Weise keiner südamerikanischen rezenten oder fossilen Form besonders nahe zu stehen, sondern vielmehr Formen aus dem Oligozän Ägyptens und Europas, die leider wie sie fast sämtlich ungenügend bekannt sind" (1926: 147–148).

For our part, we feel that there is not the slightest possibility of any special relationship between the thryonomyoids and theridomyoids. In this conclusion, we are merely reinforcing those formerly reached by Lavocat (1955). If such a relationship were to be established, we believe that it would demonstrate that the Suborder Hystricognathi was a wastebasket, because the Pseudosciuridae, the most primitive theridomyoids, had themselves only just originated in the middle Eocene, at a time when there were already definite hystricognaths in North America, and nothing is clearer than that theridomyoids never reached the New World and that Europe was isolated from the rest of the world during the period from quite early in the Eocene until early or middle Oligocene (Wood, 1977b: 100).

Although we think it is improbable that the theridomyoids were ever able to establish themselves outside Europe, we are not ready to abandon completely the possibility of a theridomyoid-anomalurid relationship. At least, the dental similarity between these two groups seems to us to be much greater than that between the theridomyoids and thryonomyoids or between the Thryonomyoidea and the Caviomorpha. In addition, both groups are hystricomorphous sciurognaths. Lavocat (1967: 498) has pointed out differences in middle ear structure between theridomyids and anomalurids, but the comparison was perforce between Quercy Phosphorites forms on the one hand and Recent ones on the other. Before coming to any final conclusion as to theridomyoid-anomalurid relationships, we would like some evidence from intermediate stages.

Upper Molars. We currently recognize thirteen identifiable named genera of Deseadan rodents (Table 8; *Luribayomys* and *Palmiramys* we regard as *nomina vana*), five of which (*Asteromys*, *Chubutomys*, *Litodontomys*, *Migraveramus* and *Xylechimys*) are known only from lower jaws. Of the other genera, the upper molars are four-crested in *Platypittamys* (Wood, 1949: Fig. 3A; 1974b: Fig. 2A), *Deseadomys* (Wood and Patterson, 1959: Fig. 4), *Incamys* (Fig. 17A,B) and *Sallamys* (Fig. 5A). All the known teeth of *Scotamys* are heavily worn, but it seems to us that the tooth pattern was likewise a four-crested one (Wood and Patterson, 1959: 315). In *Branisamys*, *Cephalomys*, *Protosteiromys* and the undescribed dasyproctid (p. 430) there is evidence of a fifth crest in the upper molars. This crest, however, was not a mesoloph, but originated from the anterior slope of the posteroloph, being what we call the neoloph. *Protosteiromys* (Wood and Patterson, 1959: Fig. 30) and *Branisamys* (Fig. 24B), in particular, seem to us to demonstrate this quite plainly. In five-crested Deseadan caviomorphs, the third crest from the front, the metaloph, even when interrupted in its course, is as high and as extended buccally as the protoloph, whereas, in five-crested Fayum genera (Fig. 30C,D,F), the third crest, which is certainly the mesoloph, is lower and less extended buccally than the protoloph. The fourth crest from the front in Fayum forms, the metaloph, is as high and as buccally situated as is the protoloph, just as is the third crest, the metaloph, in the caviomorphs.

Among known early Miocene thryonomyoids there is considerable variation in mesoloph development, the crest ranging from low and little extended buccally (*Myophiomys*, Lavocat, 1973: Pl. 42, Fig. 5; *Paraphiomys*, *op. cit.*: Pl. 26, Figs. 2–5; Pl. 44, Fig. 7) through low and moderately extended (*Andrewsimys*, *op. cit.*: Pl. 42, Fig. 4), low and well extended (*Phiomys*, *op. cit.*: Pl. 41, Fig. 6) to high and well extended (*Kenyamys*, *op. cit.*: Pl. 27, Fig. 5; *Simonimys*, *op. cit.*: Pl. 42, Fig. 3; *Epiphiomys*, *op. cit.*: Pl. 42, Figs. 1–2; and *Diamantomys*, *op. cit.*: Pl. 25, Fig. 7). This variability is what one would expect given the structural ancestry represented by the Fayum thryonomyoids. The mesoloph of five-crested thryonomyoids is an evolving, not degenerating, crest; it is a specialized character, not a primitive one.

Lavocat's charge (1973: 169) that our hypothesis that the four-crested upper molars of *Platypittamys* and other four-crested Deseadan genera were primitive skirts the possibility that the four-crested conditions could have been derived by simplification from a five-crested one is, of course, correct, but it would seem to us highly surprising if most genera that possessed brachyodont, primitive-looking cheek teeth had indulged in such a simplification. We believe that there is considerable evidence in support of our position. Even if there were no such evidence, Occam's Razor would argue against acceptance of Lavocat's contention without some supporting documen-

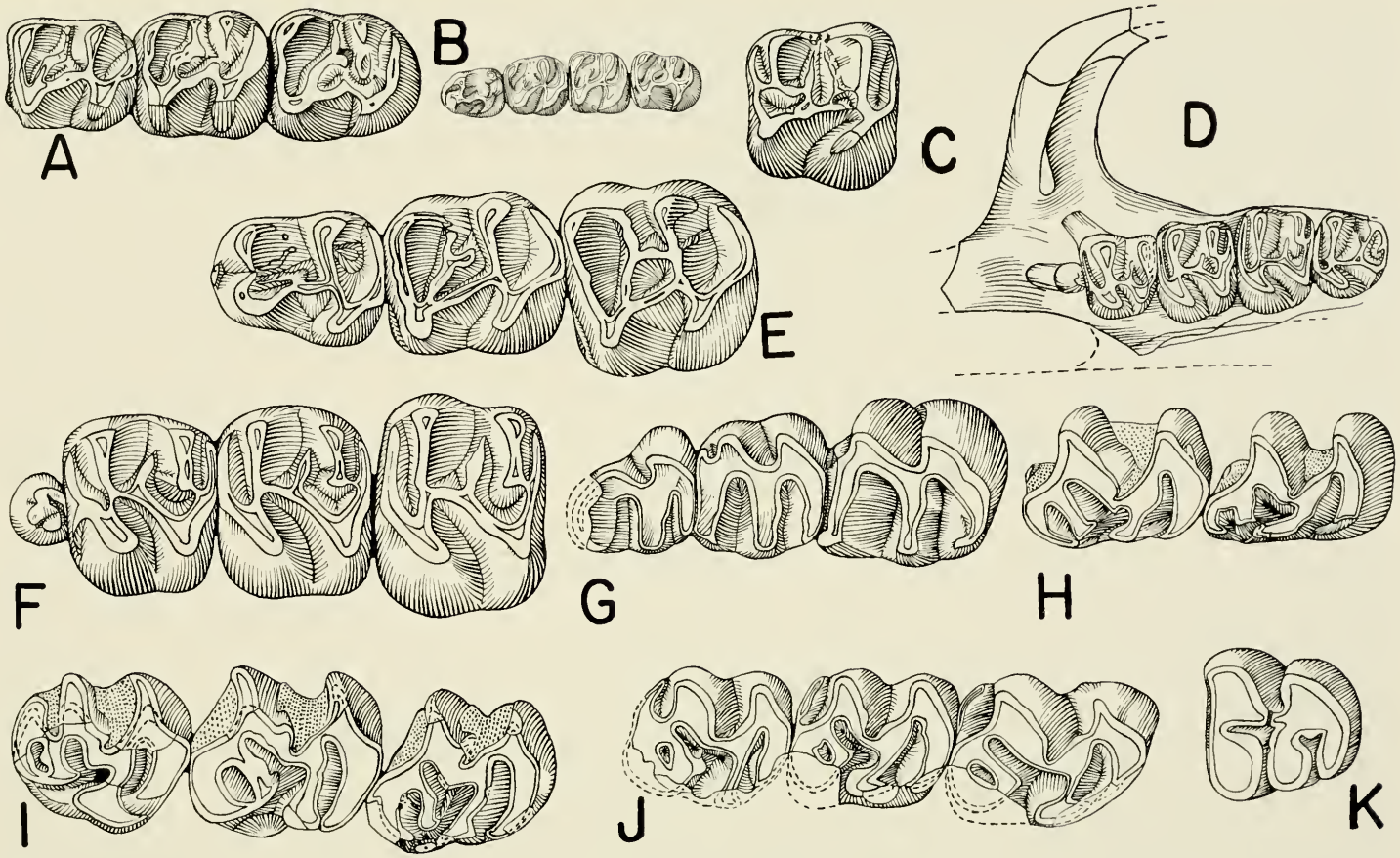

Figure 30. Cheek teeth of some Oligocene and Miocene thryonomyoids. A, C, E and F, ×10; others, ×5. A. *Phiomys andrewsi*, LM_{1-3}, YPM no. 18021; Wood, 1968, Fig. 2A. B. *P. andrewsi*, LP_4–M_3, YPM no. 18071; Wood, 1968, Fig. 1D. C. *P. andrewsi*, RM^2, YPM no. 18035, anterior end to the right; Wood, 1968, Fig. 2D. D. *Metaphiomys schaubi*, dm^{3-4}, M^{1-3}, YPM no. 21309; Wood, 1968, Fig. 6A. E. *M. schaubi*, Ldm_4–M_2, YPM no. 21310; Wood, 1968, Fig. 10E (erroneously labelled "right" in that paper). F. *M. schaubi*, Ldm^{3-4}, M^{1-2}, YPM no. 21320; Wood, 1968, Fig. 11B. G. *Neosciuromys africanus* Stromer, type, Rdm_4–M_2, Munich no. 1926x13 (=*Paraphiomys pigotti*, fide Lavocat, 1973:22). H. *Pomonomys dubius* Stromer, RM_{1-2}, Munich no. 1926x506. Dotted areas are cement. I. *P. dubius* Stromer, type, Rdm_4–M_2, Munich no. 1926x23. Dotted areas are cement. J. *Diamantomys luederitzi* Stromer, type, RM_{1-3}, Munich no. 1926x22. K. *Bathyergoides neotertiarius* Stromer, type, RM_2, Munich no. 1926x17.

tation, which we believe is entirely absent. We believe that the only basis for assuming that the caviomorph tooth pattern was derived from that of the thryonomyoids is the prior assumption that thryonomyoids were the ancestors of the caviomorphs.

If, as we believe, the Caviomorpha were descendants of franimorph reithroparamyids, their upper cheek teeth must ultimately have been derived from a four-crested ancestral stage of the type seen in *Protoptychus* (Wilson, 1937: Fig. 1) or cylindrodonts (Wood, 1973: Fig. 3), and we consider it supererogatory to assume an intermediate five-crested stage between ancestral and descendant four-crested ones until there is real evidence that such a stage actually existed.

Upper Premolars. Lavocat (1973) has greatly confused the discussion of premolar resemblances by referring to the teeth, in front of the permanent molars, indiscriminately as D (=deciduous molar) and P (=permanent premolar). In particular, he discussed the deciduous teeth of *Metaphiomys* and the probable permanent premolar of *Gaudeamus* together (1973: 170), with no indication that they were probably not homologous teeth. As a result, we do not know whether his statement that there was the "même type de prémolaire primitive dans certains Phiomyidae du Fayoum et certaines formes du Deseado" (1973: 168) was based on the comparison of permanent premolars, deciduous molars, or the deciduous molars of the African forms with the permanent premolars of the Caviomorpha. Unfortunately, although one would not get this impression from Lavocat (1973), the single tooth of *Gaudeamus* (if it is P^4 and not dm^4) is all that there is to go on as to what the upper premolars of the thryonomyoids were like, and that one tooth comes from one of the most specialized of the Fayum genera. In a later paper (Lavocat, 1978), he says very little about the antemolar cheek teeth of thryonomyoids, although he does state that P^3 or dP^3 are present in some forms (1978: 71, 78), and he included in his definition of the Family Phiomyidae (*op. cit.*: 71) the statement "Milk teeth with delayed replacement in some forms, persistent in others . . . ." He does not mention that replacement of deciduous teeth is unknown in all other thryonomyoids.

Upper premolars are known in seven of the Deseadan genera. The tooth is incipiently five-crested in *Branisamys* (Fig. 23C,F); four-crested in *Incamys* (Figs. 17A, 18C) and *Sallamys* (Fig. 4A); three-crested in *Deseadomys* (Wood and Patterson, 1959: Fig. 4A), *Cephalomys* (Wood and Patterson, 1959: Figs. 13A, 14A,B) and *Platypittamys* (Wood, 1949: Fig. 3A,B); and probably three-crested in *Scotamys*. The teeth of the three-crested forms look primitive to us, and we believe that these teeth are close to the ancestral caviomorph condition.

Upper premolars of thryonomyoids are unknown except for the one specimen of *Gaudeamus aegyptius* that is more probably P^4 than dm^4 (Wood, 1968: Fig. 14A and Table 2). All other antemolar upper cheek teeth (except for the peg-like dm^3 or P^3) known among thryonomyoids from the early Oligocene to the present are dm^4. The premolar of *Gaudeamus* is a three-crested tooth and, as Lavocat has stated (1973: 170), it shows some similarity to that of *Platypittamys* (Wood, 1949: Fig. 3A,B), although the two are far from identical and, if one were to have been derived from the other, that of *Platypittamys* seems obviously to be the more primitive in that it is much more brachyodont, the cusps are more distinct, and the crests are less fully developed. The permanent premolars of both *Platypittamys* (Wood, 1949: Fig. 3A,B; 1973b: Fig. 2A,B) and *Gaudeamus* (Wood, 1968: Fig. 14A) could have been derived from one like that of the hystricomorphous franimorph *Protoptychus* (Wilson, 1937: Fig. 1).

Lower Molars. The lower molars of *Phiomys*, the most primitive known

thryonomyoid, were shown by Wood (1968: 32–33) to vary widely as to crest number. Within this primitive genus can be found "a complete sequence from five-crested specimens of *Ph. andrewsi* through four-crested ones of the same species, to the nearly three-crested ones of *Ph. paraphiomyoides* and of *Ph. lavocati*. Since the first and last of these species are contemporaneous animals, it is possible to assume either that evolution is proceeding from five-crested to three-crested, or the reverse sequence, or from four-crested in both directions." Wood's preference was for the last of these choices: "the four-crested would be the most primitive, and evolution would be in both directions, toward simplification or complication." We adhere to this interpretation. If Wood was correct on this point, this alone would rule out any possible relationship between the thryonomyoids and the theridomyoids. It would also support the idea of parallel evolution of the Thryonomyoidea and Caviomorpha from northern hemisphere franimorphs that had four-crested molars. Among the early Miocene thryonomyoids, the number of crests is either four or three. A point that must be stressed here is that in those early thryonomyoids that were "experimenting" with five-crested lower molars, the fifth crest (the third from the front) is certainly a mesolophid; in some individuals traces of a mesoconid and (rarely) of a metastylid can be seen.

The lower molars of Deseadan rodents are generally four-crested (*Asteromys*, *Branisamys*, *Cephalomys*, *Chubutomys*, *Incamys*, *Migraveramus*, *Platypittamys* and *Protosteiromys*). In *Xylechimys* (Patterson and Pascual, 1968: Fig. 2A) and *Deseadomys arambourgi* (Wood and Patterson, 1959: Fig. 5) the teeth are intermediate between being four-crested and three-crested, and *D. loomisi* is three-crested, one of the crests, the metalophid, of the four-crested forms having been lost (Wood and Patterson, 1959: 311, Fig. 7). The teeth of *Sallamys* (Fig. 5D–F) seem intermediate in this respect between those of the two species of *Deseadomys*. The lower molars of the known specimens of *Litodontomys* and *Scotamys* are too worn to permit certain determination of the number of crests, although the teeth are compatible with there having been four. There is, therefore, no evidence that early caviomorph lower molars were ever five-crested; no known lower molar of any Deseadan rodent shows any indication of a mesoconid, a mesostylid or a mesolophid. When, as in some specimens of post-Deseadan erethizontids, an incipient fifth crest develops on the lower molars, it arises from the posterior face of the anterolophid (Wood and Patterson, 1959: 381), not from the ectolophid, and hence is completely unrelated to the fifth crest of thryonomyoids.

A striking feature of the lower molars of nearly all thryonomyoids is the presence of an anteroexternal basal cingulum. Among the Fayum forms it is present in *Phiomys* (Fig. 30A,B; Wood, 1968: Figs. 1; 2A,B; 3A,B; 4A) although very small or absent in *P. lavocati* (Wood, 1968: 47; Fig. 5A,C,D), small in *Paraphiomys simonsi* (Wood, 1968: Fig. 5F), transferred below (p. 520) to *Neosciuromys*, but large in *Metaphiomys* (Fig. 29E; Wood, 1968: Figs. 8–10, 12H, 13A) and *Phiocricetomys* (Wood, 1968: Fig. 16A,D). This last genus is peculiar among thryonomyoids in having but three lower cheek teeth, either dm_4–M_2 or M_{1-3} (see p. 521). The second tooth has a very heavy anterior cingulum that extends back along the buccal face of the tooth and the buccal half of the posterior face; cuspules occur here and there along its length. In the last tooth, the cingulum, very heavy and with cuspules, reaches posteriorly to the hypoconid, and in the first is limited to the base of that cusp. Only in *Gaudeamus*, a specialized form, is the anterior cingulum entirely lacking (Wood, 1968: Figs. 14E,G,H; 15B–E,G).

An anterior cingulum, like that of *Phiomys* and *Metaphiomys*, is very prominent among the Miocene thryonomyoids (Fig. 30G–J; Stromer, 1926: Pl. 41, Figs. 24, 25C, 32C; Pl. 42, Fig. 28; Lavocat, 1973: Pl. 25, Fig. 6; Pl. 26, Figs. 7–10; Pl. 27, Figs. 1, 3, 4, 9; Pl. 28, Figs. 1, 2, 4, 11–13). These cingula are prominent and elevated in *Petromus* (Wood, 1962b: Fig. 1E,F), but are absent in *Thryonomys* (Wood, 1962b: Fig. 2A–C) as in its probable ancestor *Gaudeamus*.

There is no trace of such a basal anterior cingulum in any bathyergoid (Lavocat, 1973: Pl. 29, Figs. 5–6; Pl. 30, Figs. 1–6), hystricid or caviomorph, so far as we are aware. This feature, by itself, it seems to us, rules out all known thryonomyoids (except *Gaudeamus*, which, of course, is much too advanced in the cresting of its cheek teeth to be a possible caviomorph ancestor) from possible ancestry to any caviomorph, hystricid or bathyergid. The presence of this cingulum on the molars of thryonomyoids means that any thryonomyoid that could, morphologically, have been ancestral to the caviomorphs must be a hypothetical Eocene form with an assumed set of characters quite different from those of any known member of the superfamily. We consider it highly doubtful that such a hypothetical form could be included in the Thryonomyoidea. We believe it would have been a franimorph. The Chapattimyidae (Hussain *et al.*, 1978) do not fill the requirements for such an ancestral form, nor do their lower teeth possess an anterior cingulum of the sort found in the Thryonomyoidea.

Lower Premolars. The lower premolars of thryonomyoids are unknown except for those described by Wood (1968: Figs. 1B,D; 14E) from the Jebel el Qatrani Formation (Fig. 30B). He was able to find only 3 permanent lower premolars (P_4) as compared with 57 deciduous ones (dm_4) in the material at his disposal. The only species in which there certainly was replacement of the deciduous tooth by its permanent successor was *Phiomys andrewsi*, the most primitive known thryonomyoid, and in this form replacement was delayed long after the normal time of replacement. The single permanent lower premolar of *Gaudeamus* was uncovered, deep within the jaw, when the deciduous tooth was removed from above it (Wood, 1968: 72); whether or not it would ever have erupted is unknown; certainly eruption would not have occurred until rather late in life. All three known Fayum specimens of P_4 are from the lower fossil wood zone and all have essentially the same pattern. There is no suggestion of an anteroconid on any of them. The metaconid is the highest element of the anterior part of the tooth, and is continued anteriorly by a cingular arm that crosses in front of the protoconid in one specimen of *Phiomys andrewsi* (Wood, 1968: Fig. 1D) and in *Gaudeamus* (*op. cit.*: Fig. 14E). There may (*P. andrewsi*) or may not (*Gaudeamus*) be a mesoconid. There is a complete ectolophid in *P. andrewsi*, but none in *Gaudeamus*. The entoconid is completely isolated in all three teeth, except from the posterolophid through which it is connected with the hypoconid.

In the Deseadan Caviomorpha, P_4 primitively had a complete ectolophid (*Asteromys*, *Cephalomys*, *Deseadomys*, *Migraveramus*, *Platypittamys* and *Sallamys*), but progressively it became interrupted (*Incamys*, Fig. 19C–E). There is no anteroconid in *Asteromys* (Wood and Patterson, 1959: Fig. 26A), *Deseadomys* (*op. cit.*: Fig. 5), *Platypittamys* (Wood, 1949: Fig. 3C–D; 1974a: Fig. 2C–D) or *Sallamys* (Fig. 5C). There is no anterior arm of the metaconid nor a mesoconid in any of these genera. The entoconid may be connected directly with the hypoconid with no posterolophid (*Platypittamys*); through the hypolophid with a distinct, isolated, posterolophid (*Cephalomys* and *Sallamys*); only through the posterolophid (*Deseadomys*); through both the hypolophid and posterolophid

(*Asteromys* and *Migraveramus*); or there may be no hypoconid-entoconid connection at all until after very considerable wear (*Incamys*).

Of all the Deseadan lower premolars, the closest to those of *Phiomys* are those of *Platypittamys*. We believe that this is because the former is close to the primitive thryonomyoid pattern and the latter close to the primitive caviomorph one, and that both the thryonomyoids and caviomorphs were descended from primitive (and hence similar) franimorph ancestors that had four-crested lower premolars. Lavocat (1973: 169–170) has argued that, in general, the cheek teeth of *Platypittamys* were not primitive. We disagree with him on this. Slightly later (*op. cit.*: 170), Lavocat stated that the structure of P_4 of *Deseadomys* and *Platypittamys* is fundamentally identical to that of *Phiomys andrewsi* and, hence (as we interpret his meaning), primitive. But we do not see how it is possible for the pattern of P_4 of *Platypittamys* to be considered to be primitive without also accepting the upper and lower molars and the upper premolar of *Platypittamys* as primitive. If this be done, the patterns of P_4 might suggest close caviomorph-thryonomyoid relationships, but the patterns of the other cheek teeth would demonstrate the absence of such affinities. We know of nothing that would interfere with the derivation of P_4 of *Asteromys*, *Cephalomys*, *Deseadomys*, *Migraveramus*, *Platypittamys* or *Sallamys* from those of cylindrodonts (Wood, 1973: Fig. 5A) or, ultimately, of *Franimys* (Wood, 1962a: Fig. 49A) or *Reithroparamys* (*op. cit.*: Fig. 42B).

Thus, while we agree with Lavocat (1973: 168) that there is the "même type de [lower] prémolaire primitive dans certains Phiomyidae du Fayoum et certaines formes du Deseado," we feel that using the similarity of premolars (based on a total Oligocene to Recent thryonomyoid sample of three teeth) and disregarding the much greater difference of pattern of the molars of the same Deseadan genera is completely unjustified.

Deciduous Teeth. The best opportunity for comparing thryonomyoid and caviomorph antemolar teeth lies in the deciduous dentition, dm_4[4]. Lavocat (1976) had available both upper and lower deciduous teeth of *Incamys* and *Branisamys*, although those of the latter were broken. Although deciduous teeth are almost universally present in thryonomyoid jaws (in fact, they are never known to have been replaced by the permanent premolar after the early Oligocene of the lower fossil wood zone), they occur at about the normal mammalian frequency among specimens of Deseadan caviomorphs. Neither upper nor lower deciduous teeth are known for *Asteromys*, *Chubutomys*, *Deseadomys*, *Litodontomys*, *Luribayomys*, *Migraveramus*, *Palmiramys*, *Platypittamys*, *Protosteiromys*, *Scotamys* and *Xylechimys*, or 11 of the 15 named Deseadan genera. Only the lower is known in *Cephalomys* and *Sallamys*; both uppers and lowers are preserved in *Branisamys* and *Incamys*. We have therefore used materials from the Colhuehuapian and Santacruzian to supplement our discussion of the Deseadan specimens.

Hoffstetter (1975: 520) cited, as a common character shared by the Caviomorpha and Phiomorpha [=Old World hystricognaths?], the frequent retention of "uno o dos premolares y/o los dientes de leche correspondientes." We are not sure which if any of these forms retain both dm^3 and P^3, since these teeth are very difficult to distinguish in rodents (Wood, 1969; 1970b: 245–246), but this is a minor point. As Hoffstetter added, this retention of antemolar teeth excludes from their ancestry those forms that had lost these teeth. But, so far as we are aware, no one has ever proposed that either the caviomorphs or any of the Old World hystricognaths were descended from, e.g.,

cricetids, and we believe that Hoffstetter here was merely setting up a straw man in order to knock it down.

Upper Deciduous Teeth. Among the Oligocene Thryonomyoidea, dm^4 is known from 11 specimens of *Metaphiomys schaubi* and one of *Metaphiomys* or *Phiomys* sp. indet. (Wood, 1968: Table 2). In all of these, the tooth is five-crested, with an anteroloph, protoloph, mesoloph and a posterior marginal posteroloph, to the middle of which is connected the end of the metaloph via the lingual end of the metaconule (Fig. 30D,F; Wood, 1968: Figs. 11, 13B). This pattern is essentially identical to that of the adjacent molars.

Hoffstetter stated (1975: 520) that "*Phiomys* presènta un reemplazo normal de dP^4 por P^4." So far as we know, this statement is entirely without factual basis, and he has apparently completely misunderstood the situation in *Phiomys* (Wood, 1968: diagnosis of *Phiomys*; 39–40, 83–84). No upper premolars or deciduous molars have with certainty been reported for *Phiomys*; the only possible example of such a tooth is one specimen of dm^4, identified as "*Phiomys* or *Metaphiomys* sp. indet." (Wood, 1968: 67, Fig. 13B). We suspect that dm^4 was replaced, late in life, by P^4, simply because the corresponding replacement occurred in the lower teeth. But this would be a long, long way from "un reemplazo normal."

In caviomorphs, dm^4 is usually very similar to the molars in crown features, but may be somewhat smaller and longer and have a larger anteroloph and paraflexus. Exceptionally, as in living dasyproctids, the anterior half of the tooth may elongate and neomorph crests develop within the enlarged parafossette.

Among Deseadan caviomorphs, the tooth is best known in *Incamys* (Fig. 17A,H,I), one specimen (Fig. 17H) being essentially unworn, and another (Fig. 17I) only slightly worn. Both of these teeth clearly consist of four transverse crests, the third of which is interrupted, with no indication of a fifth crest. We believe these crests to be the anteroloph, including the protocone; the paracone-protoconule-hypocone; the metacone-metaconule-hypocone; and the posteroloph. There is no suggestion of a mesoloph, which we feel is because the Caviomorpha were derived from North (or Middle) American franimorphs in which there never was a mesoloph. The dm^4 of *Branisamys*, figured by Hoffstetter and Lavocat (1970: Fig.) is both broken and badly worn, but suggests that there had been a four-crested pattern. However, one specimen (Fig. 24B) of dm^4 of this genus clearly shows increasing complexity. There is an incipient anterior crest arising from the buccal end of the anteroloph, and the beginning of a neoloph, arising by forward growth of ridges from the middle and the lingual tip of the posteroloph. The tooth of *Incamys* seems to us to be clearly the more primitive.

This tooth is known from a somewhat larger number of Santacruzian genera. In *Neoreomys* (Scott, 1905: Pl. 65, Fig. 3), the anterior part of the tooth seems to be similar to that of *Incamys*. There is a posterior prism of enamel, with a lake in its center, which we would interpret as being homologous to the two crests in *Branisamys* that we have called the beginnings of a neoloph. In *Eocardia* (Scott, 1905: Pl. 68, Fig. 27), the tooth has acquired the typical eocardiid outline, but would seem to be composed of the same features as in *Incamys*. Scott also figured a worn dm^4 of *Neoreomys australis* (1905: Pl. 65, Fig. 4), *Stichomys regularis* (1905: Pl. 65, Fig. 19) and *Schistomys erro* (1905: Pl. 68, Fig. 26); these, however, show essentially no details of the pattern. They could be (and probably were) based on the same basic pattern as in *Incamys* and *Branisamys*.

It is clear that the fifth crest that seems to be developing in the caviomorph dm^4

(our neoloph) is a forward outgrowth from the posteroloph—absent in *Incamys*, developing in *Branisamys* and fully developed in the Santacruzian genera. We see no possibility of homologizing this crest with the metaloph of the thryonomyoid dm^4, since the neoloph of the caviomorphs was clearly in the process of development, in South America, during the Oligocene.

A tooth that is probably dm^3 rather than P^3 is represented by an alveolus in the type of *Branisamys luribayensis* (Hoffstetter and Lavocat, 1970: Fig.) and in PU no. 21955 (Fig. 24B); an intra-alveolar root in *Incamys bolivianus*, PU no. 20980 (Fig. 17I); and a worn nubbin on both sides of the skull of *I. bolivianus*, PU no. 21726 (Fig. 17A). These tell us nothing other than that a minute tooth was present. One was also present in *Metaphiomys schaubi* (Fig. 29D; Wood, 1968: Fig. 11B, Table 2); no trace of such a tooth is preserved in *Gaudeamus*. The presence of this tooth is merely a primitive rodent character. At present, we do not know, for any of the genera involved, whether this tooth was dm^3 or P^3 (Wood, 1970b: 245–246), or whether it had a pattern or was merely a conical cusp.

Lower Deciduous Teeth. The lower milk molar (dm_4) is better represented among the Deseadan Caviomorpha than is the upper, but still is known only from four genera: *Branisamys*, *Cephalomys*, *Incamys* and *Sallamys*. All three available teeth of *Incamys* are highly worn; there is no way of being certain whether the pattern was like that in the other genera, or whether it was different. The Princeton collections include a specimen of *Branisamys* with a broken dm_4 (Fig. 24G), and we believe that GB no. 014, the type of Hartenberger's *Villarroelomys bolivianus* (Figs. 26A, 31H) is also dm_4 of *Branisamys*. According to our interpretations, the pattern in both of these *Branisamys* teeth was essentially like that of *Sallamys* (Figs. 5D, 31F) or of *Cephalomys* (Figs. 26B, 31G).

The pattern of dm_4 of *Sallamys pascuali* posed a number of problems that we have touched on above (p. 390). This tooth (Figs. 5D, 31F) is obviously very complex, and closely resembles that of *Cephalomys* (Wood and Patterson, 1959: Fig. 20A,B), the only previously described unbroken Deseadan dm_4. In each, the talonid is like that of the molars, the hypoconid being continuous backward into the posterolophid and forward into the hypolophid. It is in the very complex trigonid that the differences lie. There is a continuous anteroposteriorly directed ectolophid; a cusp that we believe to be the protoconid extends backward toward the entoconid. In *Cephalomys* (Fig. 31G), the metaconid lies behind the protoconid, whereas in *Sallamys* (Figs. 5D, 31F) it is farther forward. In both, the anterior end of the tooth is formed of a multicuspidate complex that we consider to have been derived from the anteroconid. A complex anteroconid area is a rather frequent evolutionary trend in dm_4 of a wide variety of unrelated rodents.

An attempt to unravel the homologies of the parts of the teeth in these two forms has led us into an investigation of the lower deciduous teeth of later caviomorphs.

In the simplest type of caviomorph dm_4 that we have seen, the trigonid consists of buccal (protoconid) and lingual (metaconid) cusps, connected posteriorly through a metalophid and anteriorly through an anterolophid (in which the anteroconid may or may not possess some individuality), surrounding a trigonid basin or anterofossettid (*Erethizon dorsatum*, Fig. 31A). Due to the greater length of the tooth, this fossettid is larger than its serial homolog in the molars. This complex is united with the talonid by the ectolophid.

Deciduous lower molars of this sort are known in such octodontids as *Sciamys*, in early erethizontids, and in various echimyids, such as *Prospaniomys* (Figs.

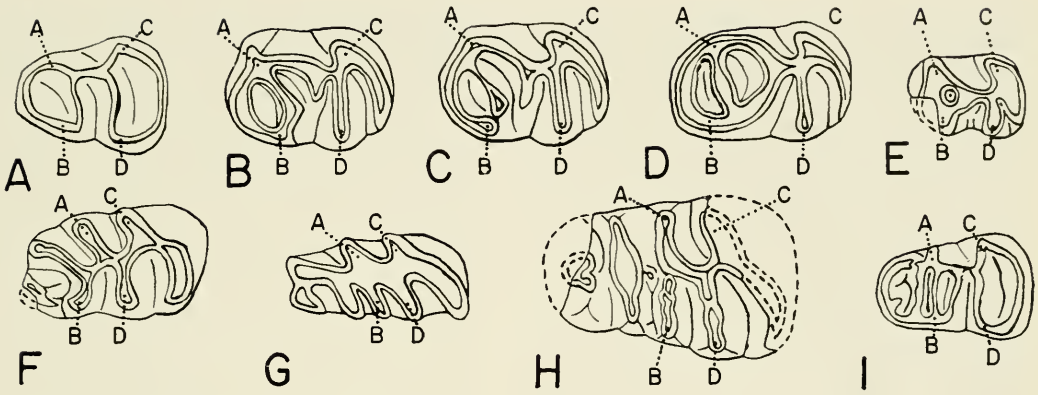

Figure 31. Sketches of lower deciduous molars (dm_4) of selected caviomorphs, not to scale; all drawn as if from the right side. A. *Erethizon dorsatum*, MCZ no. 51367. Simple pattern. B. *Protacaremys prior*, AMNH no. 29707. C. *P. prior*, FMNH no. P 13295. D. *P. prior*, AMNH no. 29692, reversed. E. *Prospaniomys priscus*, AMNH no. 29697, reversed. F. *Sallamys pascuali*, PU no. 20909. G. *Cephalomys arcidens*, ACM no. 3013. H. *Branisamys luribayensis* (type of *Villarroelomys bolivianus*), GB 014, reversed and restored. I. *Erethizon dorsatum*, MCZ no. B 7752. Complex pattern.

Abbreviations: A—protoconid; B—metaconid; C—hypoconid; D—entoconid.

5H, 31E), as variants in *Acarechimys* (for validation of this name, see Appendix 2), in *Eumysops* (Kraglievich, 1965: Fig. 2) and in the Antillean heteropsomyines (Miller, 1929: Pl. 2, Figs. 3a, 4a; Pl. 3, Fig. 1a; Pl. 4, Fig. 2a).

There have been various modifications of this pattern, ranging from relatively simple to highly complex. As examples of simple changes, we may cite: *Paradelphomys*, in which the very marked obliquity of the lophids has converted the circular anterofossettid into a slit and has greatly shortened the ectolophid without completely obscuring the primitive pattern; and *Spaniomys*, *Stichomys*, *Cercomys*, etc., in which an anteroflexid has developed between metaconid and anterolophid, thus converting the tooth into as good a replica of the molars as the upper milk tooth usually is.

Considerably greater complexity is present in *Protacaremys prior*, although AMNH nos. 29692 and 29707 and FMNH no. P 13295 are all different in details. Here there are three crests from the protoconid to or toward the metaconid (Figs. 5G, 31B–D). The anterior of these is clearly an anterolophid; the nature of the others is more uncertain. However, on the basis of variants seen in *Erethizon dorsatum*, as discussed below, we believe the posterior crest to be a metalophid resembling the mesolophid of thryonomyoids and the middle crest to be a neomorph crossing the anterofossettid. We believe that the tooth pattern of this tooth of *Prospaniomys priscus* (Fig. 31E) is basically the same.

This stage is continued, morphologically, in *Sallamys pascuali* (Figs. 5D, 31F), where the protoconid has become separated from the metalophid, and a deep buccal valley has developed as a neomorph, as has also the anteriorly facing opening, leading deep into the anteroconid. The teeth of *Cephalomys* (Figs. 26B, 31G; Wood and Patterson, 1959: Fig. 20A) and *Branisamys* (Figs. 26A, 31H) demonstrate continuations of this process, with the anteroconid now separated from the metaconid.

This description is, of course, an attempt to present a morphological series and not a phylogenetic proposal. It is obvious that there is a great deal still to be

learned of deciduous tooth evolution in the early caviomorphs. We have presented our interpretation (Fig. 31) of the patterns of these teeth, suggesting one manner by which the pattern of *Sallamys*, *Cephalomys* and *Branisamys* could have been derived. We feel no great confidence in the complete accuracy of our interpretation, but, with our present lack of knowledge, it is as logical as any other.

Any interpretation of the actual evolution of dm_4 in the Caviomorpha is complicated by the extreme variability that we have observed in this tooth among Recent specimens of *Erethizon dorsatum*. Some individuals of this species (e.g., MCZ no. 51367, Fig. 31A) have the simplest caviomorph dm_4 that we have seen. There may be an anterior spur into the anterofossettid (MCZ no. 39006), a small swelling on the ectolophid (MCZ no. 39010), or a short spur in this location (MCZ no. B9975). The structures on these last two specimens look for all the world like an incipient mesoconid and an incipient mesolophid, respectively. The spur into the anterofossettid may form a continuous lophid that divides the anterofossettid into two (MCZ no. B7752, Fig. 31I), and may be joined by a secondary spur to produce three divisions of the anterofossettid (MCZ no. 8846). The apparent mesolophid may extend to the lingual margin of the tooth, where it may be connected to the posterior tip of the metaconid (Fig. 31I). There may be a second spur behind the apparent mesolophid (MCZ no. 7800). All intermediate stages in these developments are present in the MCZ collections, often within what were surely interbreeding populations. We feel complete confidence that dm_4 of MCZ no. 51367 (Fig. 31A) is a primitive tooth, and that dm_4 of MCZ no. B7752 (Fig. 31I) is a highly specialized one.

Although we do not know, we strongly suspect that this condition of extreme variability in dm_4 of *Erethizon* is a very recent development, perhaps related to the rapid spread of the genus over a broad expanse of North America in postglacial time. The more complex examples of dm_4 discussed above surely are in the process of developing a variety of neomorph crests, which, although sometimes resembling mesoconids and mesolophids, can only have developed as parallelisms to such structures in any other rodents.

The pattern of dm_4 of the Oligocene petromurids (see below, p. 523, for our usage of this term) is quite different. The rear of the tooth is the same as in the caviomorphs and other rodents, formed of the hypoconid connected anteriorly with the entoconid and posteriorly with the posterolophid. There is also a continuous anteroposterior ectolophid. But the anterior portion of the tooth is strikingly different. The anteroconid is a very minor feature of dm_4 (Wood, 1968; Figs. 1F,G; 2B; 3A,B; 4A; 5C; 8A; 9A–D; 10A,E; 12F); either the trigonid basin opens forward, or there is a deep valley between the protoconid and metaconid, which are near the front of the tooth; and there is usually a strong mesolophid (Wood, 1968: Figs. 1F,G; 2B; 8C; 9B–D; 10E; 14D,G; 15E,G), similar to the structure that apparently developed very recently in this tooth of *Erethizon*. Occasionally, the mesolophid is absent in the Fayum genera, although there is still usually a mesoconid (Fig. 30E; Wood, 1968: Figs. 3A,B; 4A; 5C,F).

Among the Miocene thryonomyoids, *Neosciuromys africanus* (Fig. 30G), *Elmerimys* and *Myophiomys* (Lavocat, 1973: Pl. 28, Figs. 11–13) have very simple dm_4, with a protoconid and metaconid connected through the anterior cingulum, but not through a metalophid. This is very similar to dm_4 of the Oligocene *Neosciuromys simonsi* (Wood, 1968: Fig. 5F), and is somewhat simpler than dm_4 of *Paraphiomys stromeri* or *P. pigotti* (Lavocat, 1973: Pl. 26, Figs. 7–10). The anterior portion of dm_4 is unknown in *Simonimys* (Lavocat, 1973: Pl. 27, Fig.

1) and does not show in the figure of *Kenyamys mariae* (Lavocat, 1973: Pl. 27, Fig. 6).

Only in *Diamantomys luederitzi* (Lavocat, 1973: Pl. 25, Fig. 6) and *Pomonomys dubius* (Fig. 30I) is dm_4 complicated. Here there are two or three cusps in the metaconid-anteroconid area, although they are very different from anything found in the Caviomorpha.

However, in the thryonomyid *Gaudeamus*, dm_4 is formed of a series of parallel transverse ridges, more like what is seen in dm_4 of *Theridomys* (Wood and Patterson, 1959: Fig. 35B) than like that in any caviomorph, where the closest approach we have seen to it is the complex Recent *Erethizon dorsatum* (Fig. 31I) or *Branisamys* (Fig. 31H). As in the Caviomorpha, the talonid is of the type usually (but not in *Gaudeamus*) found in the molars, but there has been extensive modification of the anterior portion.

Although there is similarity between dm_4 of *Gaudeamus* or of *Thryonomys* (Wood, 1962b: Fig. 2A) and those of caviomorphs, similarities as great or greater can be found elsewhere among the rodents. There is little or no difference between dm_4 of these thryonomyids and that of *Anomalurus* (Wood, 1962b: Fig. 1B); and dm_4 of the entoptychine geomyids *Gregorymys curtus* (Wood, 1936a: Fig. 13) and *Entoptychus* cf. *minor* (Rensberger, 1971: Pl. 6, Fig. i) or of *Theridomys* (Vianey-Liaud, 1972: Fig. 1) seem to us to be much closer structurally to those of the Deseadan Caviomorpha than are those of the thryonomyids. The pattern of dm_4 of thryonomyids is also reminiscent of that of *Theridomys*, but again we do not believe that it indicates thryonomyoid-theridomyoid affinities, as *Gaudeamus* is quite advanced for an Oligocene thryonomyoid, and the similarities of its dm_4 to that of *Theridomys* must be pure parallelisms, *Gaudeamus* having evolved from something like *Phiomys*. The patterns of dm_4 of the petromurids are very suggestive of those of various ctenodactylids (Wood, 1977a: Fig. 5). Needless to say, we do not consider either the entoptychines or the theridomyids closely related to the caviomorphs, nor the theridomyids and ctenodactylids to the thryonomyoids. We have merely selected examples of similar deciduous teeth in unrelated forms.

We do not see that the patterns of the deciduous teeth give any support to thryonomyoid-caviomorph relationships.

The great variability in dm_4 within the single living species *Erethizon dorsatum*, as well as that in *Phiomys* and *Metaphiomys* (Wood, 1968: Figs. 1F,G; 2B; 3A,B; 4A; 5C; 8C; 9A–D; 10A,E; 12F) shows what extremes of variability may occur when, for some reason, there is either strong selection toward increasing the complexity of a tooth, or a sudden reduction in selective pressures of any sort acting on it. We believe that this situation demonstrates our ignorance of many of the causes of evolutionary change in dm_4.

It is obvious from the above that not enough is known about lower deciduous teeth of caviomorphs to be of great significance in unravelling their interrelationships. As an aside, the evolutionary history of the deciduous teeth has been sadly neglected, not only among rodents, but in all of the Mammalia.

(18) *Multiserial Incisor Enamel* (by A.E.W.). Among rodents, there are three types of incisor enamel: the pauciserial, the primitive type, found in most Eocene rodents; and two more evolved types, uniserial and multiserial, found in later rodents (Korvenkontio, 1934). The temporal distribution of the three types makes any other relationship among the three very difficult to visualize.

"Pauciserial enamel is a good structural predecessor for uniserial and multiserial enamel. It would appear to be the ancestral condition .... Presumably acquisition of two layers in which the organization of prisms is different served in some way to strengthen the enamel .... There is no available evidence to suggest

that one of the two surviving kinds is superior to the other or that one of them has ever evolved from the other" (Wahlert, 1968: 13). As indicated, there are no known cases of transition between uniserial and multiserial enamel, but, in a few cases, transitional stages between pauciserial and the advanced types have been found.

In pauciserial enamel, the inner layer consists of prisms that may or may not be organized into lamellae. The bands are of variable width, the widths lying in general between those of the uniserial and multiserial types (Wahlert, 1968: 4). "The structure appears similar to multiserial enamel but lacks the uniformity of organization. Bands are usually not inclined .... Some pauciserial enamels have fewer prisms per band, and thus the bands are narrower, suggesting uniserial enamel in appearance."

The bands of the inner layer of multiserial enamel are many prisms wide. They are inclined at considerably greater angles toward the wear surface of the tooth; the values given by Korvenkontio (1934: 116–123) vary from 10° to 45° in the upper incisor and from 22° to 50° in the lower.

In uniserial enamel, the bands of the inner layer are one enamel prism wide. These are inclined toward the tip of the tooth at angles that vary more than do those of multiserial enamel, ranging from 0° to 50° in both upper and lower incisors (Korvenkontio, 1934: 116–123). The uniserial type is more highly organized than either of the others, and rather strikingly different in appearance from the pauciserial, whereas "the structure [in pauciserial enamel] appears similar to multiserial enamel but lacks the uniformity of organization" (Wahlert, 1968: 4). For illustrations of the three types of enamel, see Korvenkontio, 1934: Pls. 3–27; Wahlert, 1968: Fig. 1.

The multiserial type is present, so far as has been determined, in all caviomorphs, all thryonomyoids, hystricids and bathyergids as well as in *Pedetes* and Oligocene to Recent ctenodactylids. In the anomalurids, the enamel is uniserial.

The enamel of the upper incisor of *Protoptychus* "appears to be pauciserial. Pauciserial and multiserial enamels are similar, and a transverse section is not ideal for distinguishing them" (Wahlert, 1973b: 4). In *Prolapsus*, both upper and lower incisors were pauciserial, but the bands of the lower incisors were inclined at an angle of 19° and those of the uppers at an angle of 15° (Wood, 1973: 27). That is, the enamel of *Prolapsus* was in the process of making the transition from pauciserial to multiserial.

Recently, a group of isolated teeth of ctenodactyloids has been described from the middle Eocene of Pakistan, as members of a primitive ctenodactyloid family, the Chapattimyidae (Hussain *et al.*, 1978). Isolated incisors, referred to this family, were sectioned (*op. cit.*: Pl. 7, Figs. 1–3) and studied with the scanning electron microscope. The figures clearly show a diagrammatical pauciserial pattern (cf. Hussain *et al.*, 1978: Figs. 1–3 and Wahlert, 1968: Fig. 1C), in spite of their having been identified as multiserial (Hussain *et al.*, 1978: 104). Sahni (1980: 23) also concluded that these incisors possessed pauciserial enamel.

The presence of pauciserial enamel in what are undoubtedly ctenodactyloids (very possibly ctenodactylids) from the Eocene of Pakistan is of considerable importance in demonstrating that, even if there should turn out to be a distant relationship between ctenodactyloids and hystricognaths (which is an unproven hypothesis), multiserial enamel must have originated in the ctenodactylids independently of its origin in the various hystricognath groups. The suggestion by Hussain *et al.* that their Chapattimyidae were ancestral to the Hystricognathi, including the cylindrodonts, as well as the Ctenodactylidae, is discussed below (p. 515) and rejected.

As with so many of the important mor-

phologic features that characterize the hystricognaths, there is a shortage of fossils representing the intermediate stages between the primitive (pauciserial) and advanced (multiserial) condition. In fact, the closest things to such intermediates that we have encountered are the incisors of *Prolapsus* and *Cyclomylus*.

We believe the presence of multiserial incisor enamel in all living hystricognaths cannot be taken as evidence of the descent of the Caviomorpha from the Thryonomyoidea, especially since the only known possible transitions from typical pauciserial to multiserial enamel are those found in the franimorph *Prolapsus* and in the primitive tsaganomyid *Cyclomylus*.

(19) *Ectoparasites* (by A.E.W.). Traub has recently (1980) reviewed the zoogeography of mammalian fleas (Order Siphonaptera), chewing lice (Order Mallophaga) and sucking lice (Order Anoplura), and its implications for the relationships and past geographic distributions of their hosts. Although his conclusions are stated as being supportive of an African origin for the Caviomorpha, a careful study of his text indicates that his data do not permit one to choose between transatlantic rafting of caviomorph ancestors and descent of both the Caviomorpha and the Old World hystricognaths from Eocene franimorphs with a Holarctic distribution.

The Anoplura infest sciurids, heteromyids, cricetids including gerbils and microtines, murids, dipodids, caviids, chinchillids, echimyids, bathyergids, *Pedetes* and *Thryonomys*, as well as lorises, lemurs and tupaiids. Traub considered (1980: 127–133) that these lice originated in North America, infested rodents as soon as the latter appeared, and spread through most groups of the order. He believed that the anopluran families probably date from the initial differentiation of the rodents. In fact, even the genus *Polyplax* may well be that old, since it "infests rodents (and occasionally other hosts as well) in most parts of the world, infesting such theraphions as phiomorphs like bathyergids and thryonomyids; caviomorphs like caviids, chinchillids and echimyids; dipodids; pedetids; the only true cricetids in the Ethiopian region; other cricetid rodents elsewhere; xerines and other sciurids; heteromyids; loricids; lemuroids; tupaioids; and leporids. The majority of these associations are surely primary" (Traub, 1980: 131). This suggests the possibility that *Polyplax* as a genus may date from the Eocene or Paleocene.

The distribution of the rodent Anoplura fits well with a North American (or Asiatic) origin of the order, and a worldwide distribution on and with the rodents. There are some peculiarities in their known distribution, probably due to a careful search not having been made of all possible hosts, but the data do not seem to me to give any support to an African origin of the Caviomorpha in preference to a North (or Middle) American origin.

One suborder of Mallophaga, the Amblycera, are primarily parasites of marsupials, with one family, the Boopidae, restricted to Australia and another, the Trimenopomidae, largely South American but extending into Central America (Traub, 1980: 122–127). A third family, the Gyropidae, are also South American, and perhaps were derived from the Trimenopomidae. The trimenopomids infest members of the Caviidae, Chinchillidae and Echimyidae, as well as marsupials, and the gyropids are found on these caviomorph families and the Dasyproctidae (Traub, 1980: 122), but both families are apparently absent on the Erethizontidae, Octodontidae, Abrocomidae, Hydrochoeridae, Dinomyidae and Cuniculidae. Clay (1970: 94–96) suggested that when the ancestral caviomorphs reached South America they had no amblyceran parasites; that they acquired trimenopomids from South American marsupials; that these then evolved

into a distinct family, Gyropidae, on the caviomorphs; and that this was followed by another caviomorph infestation by other trimenopomids from South American marsupials. Certainly the Amblycera have no bearing on the origin of the Caviomorpha other than to suggest that these rodents came to South America from somewhere else.

"While members of the family Trichodectidae (suborder Ischnocera [Order Mallophaga]) are legion on fissiped Carnivora, Perissodactyla, Artiodactyla and Hyracoidea, they are found on only two groups of rodents, viz. an isolated branch occurring on the caviomorph Erethizontidae (New World porcupines) and a second distinctive taxon on the geomyids . . ." (Traub, 1980: 122). Traub gives no indication as to whether these lice were found on North American or South American erethizontids. However, the family clearly is primarily non-rodent and would seem to have a fundamentally Holarctic distribution. The erethizontids presumably acquired the lice from carnivores, perissodactyls or artiodactyls either in South or in North America, and the geomyids would have done the same in North or Middle America. The trichodectids therefore would seem to have no bearing on the origin of the Caviomorpha, except that they ultimately had a northern origin.

The fleas are a more complicated matter, both as to their own classification and as to their import for the relationships of their hosts. Traub believed (1980: 157) that fleas were in existence on Pangea and were represented from their separation on both Gondwanaland and Laurasia. He believed that the major flea families originated on the various continents presumably early in the Cretaceous, and that the subfamilies of modern fleas probably originated in the Cretaceous (1980: 113). The presence of the modern genus *Palaeopsylla* in the Baltic Amber of Europe shows that flea genera are very long-lasting, and thus infestation by members of a single genus of fleas does not indicate that two populations of mammals may not have been separated also for a very long time. Furthermore, another modern genus, *Ctenophthalmus*, according to Traub (1980: 143) is apparently the immediate ancestor of *Palaeopsylla*, so that it must be even older. It does not seem surprising, in that case, that *Ctenophthalmus* has a geographic distribution that is not at once readily understandable.

The large flea family Heteropsyllidae was apparently of northern (Laurasian) origin (Traub, 1980: 157). Some of its derivative subfamilies and tribes are South American and one is also Australian. One subfamily, the Ctenophthalminae, includes four tribes, two Neotropical, one Nearctic and one Holarctic and Ethiopian. Traub has suggested that these are indications of the African origin of the Caviomorpha, but, if one accepts the antiquity of flea taxa mentioned above, these data seem as readily explicable by having the infestations of the Caviomorpha and the African hystricognaths date from their common Eocene franimorph ancestors, who reached South America and Africa by independent routes.

Therefore, although Traub's conclusions read as though it is necessary to assume a transatlantic migration of caviomorph ancestors to explain the present distribution of the ectoparasites, I do not believe that this necessarily follows from his data. Traub informs me (letter dated Feb. 27, 1981) that "We are not as far apart on African-South American connections as our earlier correspondence may have indicated."

(20) *Other features* (by A.E.W.). There have been certain other supposed evidences of direct caviomorph-thryonomyoid relationships that were not cited by Lavocat (1973), but which were specified by Lavocat (1971a) or Hoffstetter (1975: 521, 522). These include the presence of a sacculus urethralis, serology, and fetal membranes, subjects concerning which

we feel that we cannot speak with any authority. We do not discuss these here, since we feel that we have previously (Wood and Patterson, 1959: 391–392; 413—414 and 414, n. 34; Wood, 1974b: 47–49; 1975a: 76–77 and Fig. 1; 1977a: 135) said everything that can be said on these topics until further evidence is produced by specialists in the various fields.

Recently, Sarich and Cronin (1981) have discussed rodent molecular systematics, concentrating on cricetids and hystricognaths. They mention, as one problem in this connection (*op. cit.*: 407) the "poor fossil record" of rodents, which might have been true a half century ago, but certainly is not today. They feel (1981: 419) that cricetids, "given their total absence in the appropriate North American fossil record, are, then, almost certainly of African origin . . . we see no great problem in having several cross the Atlantic in the late Eocene and early Oligocene from Africa to . . . South America." This total absence of cricetids from the Oligocene and Miocene of North America will come as a surprise to most mammalian paleontologists, as will the suggestion that they originated in Africa, where they are unknown in the Oligocene and rare in the early Miocene. Sarich and Cronin (1981: Fig. 7) illustrate their ideas of how the cricetids moved from Africa to South America to North America.

In discussing the hystricognaths, Sarich and Cronin mention (1981: 410) the "total lack of hystricognaths . . . in North America (except, of course, for the recent migrant *Erethizon*," apparently disregarding the description of hystricognathy in *Prolapsus* (Wood, 1972; 1973) and *Guanajuatomys* (Black and Stephens, 1973). They develop a molecular phylogeny of the Hystricognatha, with two groups, one including *Hydrochoerus*, *Cavia*, *Erethizon*, *Dasyprocta* and *Chinchilla*, and the other *Hystrix*, *Bathyergus* and *Petromus* (these two closely related), *Hoplomys*, *Proechimys*, *Myocastor*, *Octodon* and (probably) *Capromys*, *Geocapromys* and *Plagiodontia*. These two groups, they believed, crossed from Africa to South America separately, probably (although this point is not specifically made by them) after the invasion of South America by the cricetids.

A final surprise to a rodent paleontologist is Sarich and Cronin's mention (1981: 419) of "ancient murids in Australia . . . ."

In view of all the misconceptions that these authors were laboring under as to the fossil record of rodents, and the impossibility that their ideas of cricetid relationships are correct, there seems to me to be no reason why their data on hystricognath relationships could not fit equally well with our thesis of the origin of the suborder in some part of Holarctica and their subsequent invasion of South America from Middle America and of Africa from southwestern Asia, as with their proposal of multiple transatlantic hystricognath migrations from Africa to South America.

(21) *Summary* (by A.E.W.). As we have tried to make clear in this section, there are obvious similarities and obvious differences between the Caviomorpha and the Old World Hystricognathi. There is, however, not a single feature that characterizes all members of these two groups and that is found nowhere else among the rodents.

In our opinion, the most basic features (hystricognathy and the anterior deepening of the pterygoid fossa) are resultants of the lengthening of *M. pterygoideus internus*. The former occurs, incipiently to fully developed, among franimorphs. The condition of the pterygoid fossa is unknown in these forms; we suspect that it had deepened variable amounts. The dorsal opening of the fossa, in geomyoids, *Spalax* and *Aplodontia*, is presumably the result of parallelism. We suspect that these two characters (or rather, the lengthening of *M. pterygoideus internus* which caused them) are the only

valid diagnostic features of the Hystricognathi.

There are a number of respects in which the Bathyergoidea are quite different from most or all other hystricognaths. These include their protrogomorphy (except *Bathyergoides*, which was hystricomorphous in a manner *sui generis*); the rather distinctive ear ossicles and their much greater fusion than in any other rodents; the absence of gyrencephaly; and their very different nematodes.

Three features separate the Erethizontidae from all other modern hystricognaths—the structure of the middle ear, the presence of an internal carotid artery, and the serology. These last two are so distinctive that the students of these subjects felt that the Erethizontidae deserve a separate sub- or infraorder of their own.

A number of features are shared with the completely sciurognathous ctenodactylids—hystricomorphy, fusion of malleus and incus, multiserial incisor enamel, and perhaps a sacculus urethralis. The ctenodactylids, however (Wood, 1977a), clearly have an ancestry entirely independent of that of the hystricognaths.

In several features, some or all of the Caviomorpha are clearly more primitive than any known Old World hystricognath, supporting the derivation of the Old World forms from the New, but making the reverse derivation difficult to accept. These include the rather widespread occurrence of non-fusion of the ear ossicles among caviomorphs, the presence of an internal carotid artery in the erethizontids, the four-crested molars of the primitive caviomorphs, and the universal replacement of dm_4 in the Deseadan caviomorphs. *Platypittamys* has less well-developed hystricomorphy than any known thryonomyoid or hystricid.

The ascending process of the alisphenoid has been reduced in living hystricognaths, though to a lesser extent in the bathyergids than elsewhere; its condition is unknown among franimorphs. A similar reduction characterizes muroids.

The amount of gyrencephaly is greater among hystricognaths than elsewhere in the order. However, as pointed out above (p. 490), gyrencephaly is merely a secondary result of increase of brain size, and a greater proportion of hystricognaths than of sciurognaths have attained large size.

A number of the features cited by Lavocat and Hoffstetter do not seem to us to have any significance whatsoever. These include the jugal fossa, generally absent and highly variable when present; the heaviness of the malar and the sinuosity of its anterior suture, both extremely variable and not confined to hystricognaths; the lateral strip of the supraoccipital, randomly present throughout the Rodentia; the cleft between the bulla and the squamosal, varying in its development from large to absent; the development of the maxillary on the floor of the orbitotemporal fossa, which does not differ in any respect from the primitive rodent condition; and the exceedingly variable retention of an independent interparietal.

It seems to us to have been demonstrated that the known thryonomyoids were morphologically incapable of having given rise to the Caviomorpha, and that the evolutionary trends within the thryonomyoids were such that it would be difficult to envisage any near ancestor that could have had such capabilities.

Some authors (e.g., Sarich and Cronin, 1981) have adopted the point of view that any evidence indicating a closer relationship of Old World and New World hystricognaths to each other than to any sciurognaths is evidence in support of transatlantic rafting of caviomorph ancestors, ignoring the fact that such a closer relationship would be just as expectable under our hypothesis of the derivation of the Caviomorpha from Middle American Eocene franimorphs.

We feel that these results indicate that the Suborder Hystricognathi is a reasonable concept; that the Caviomorpha and Bathyergoidea originated from the Fran-

imorpha independently of the Hystricidae and Thryonomyoidea; and that there has been extensive parallelism among the later hystricognath groups after their separation from their Holarctic franimorph Eocene ancestors.

The Classification of the Suborder Hystricognathi

THE SUPERFAMILIES OF THE CAVIOMORPHA

It is rather generally agreed that there are four major groups within the South American Caviomorpha. This was first clearly recognized by Simpson (1945: 94–99, 209–213), who proposed four superfamilies: Erethizontoidea (Erethizontidae), Octodontoidea (Octodontidae, Ctenomyidae, Abrocomidae, Echimyidae, Capromyidae), Chinchilloidea (Chinchillidae) and Cavioidea (Eocardiidae, Caviidae, Hydrochoeridae, Dasyproctidae, Dinomyidae and Heptaxodontidae). Apart from various shufflings (the *Acaremys* group to the Octodontidae, the *Eumegamys* group to the Dinomyidae) and changes in rank (elevation of the Cuniculinae to family, lowering of the Ctenomyidae and Capromyidae to subfamily), about which there is inevitably less agreement, his arrangement has stood in its essentials. In our study of the Patagonian Deseadan rodents (Wood and Patterson, 1959) we stressed that the erethizontids occupied an isolated position in relation to the rest, and supported the removal of the dasyproctids, dinomyids, cuniculids and heptaxodontids from the Cavioidea, transferring them to the Chinchilloidea.

In recent years several publications dealing wholly or in part with Recent hystricognaths have appeared: Gorgas (1967) on the stomach and intestinal canal; Bugge (1971, 1974a, 1974b) on cephalic arteries; Woods (1972, 1975) on jaw, hyoid and fore limb musculature; Woods and Howland (1977) on the skin musculature; and George and Weir (1974) on chromosomes. Despite the unavailability of numerous forms, some of them critical, to one or another of these authors, much new information pertinent to caviomorph higher taxonomy has been made available by their studies.

The distinctness of the erethizontids is fully confirmed, all the new evidence separating them clearly from the other caviomorphs. Bugge, as did Moody and Doninger (1956: 52–53) before him, believed that they merit a sub- or infraorder of their own, and has proposed the Suborder Erethizontomorpha for them (1974a: 56, 70, 71, 73). He did so primarily on the basis of their retention of an internal carotid artery, a primitive structure that has been lost in all other living hystricognaths. It is difficult for us to assess the significance of this. Of the Deseadan rodents, the basicranial region is known only in *Incamys*, and here there is what might be a carotid foramen (p. 411). Apparently this area is preserved in a skull of *Branisamys*, SAL 102, but is still buried in matrix (Lavocat, 1976: Pl. 2, Fig. 1). The skull of the Fayum thryonomyoids is unknown except for maxillary fragments. It is possible, therefore, that Oligocene hystricognaths possessed this artery (*Reithroparamys* has what is, topographically, a carotid canal—Wood, 1962a: 122), and that only the erethizontids have retained it to the present. To further complicate matters, as indicated above (p. 485), possession of a "carotid" foramen by a rodent does not prove possession of an internal carotid artery (Wahlert, 1974a: 373).

In view of all of these uncertainties—and we believe that we are in very close agreement with Lavocat (1976: 82–83) regarding them—we doubt if possession of an internal carotid by erethizontids can safely be adduced to prove their separation at a sub- or infraordinal level. For the present at least, we retain them as a superfamily of the Caviomorpha, stressing, as we have before, that they were in all probability a very early offshoot from the ancestral stock.

Lavocat (1976: 82) wrote: "En raison

des traveaux de J. Bugge . . . Wood (1975) admet actuellement que les Erethizontidae pourraient être assez distants des autres Caviomorphes." This was "admitted" much earlier (Wood and Patterson, 1959: 377, 391–392). What Wood did state (1975a: 77) was that, if Bugge was correct in his concept of Erethizontomorpha, two invasions of South America would be required, the implication being that visualizing multiple successful transatlantic raftings became exceedingly difficult, and that North America was hence the more likely source area.

The coherence of the Octodontoidea is not called in question by the new studies of Recent forms. Unfortunately, too few of the numerous echimyid genera were available to the various authors to provide evidence with which to test the arrangement of the echimyid subfamilies suggested above (Fig. 6). Woods (1972: 190) found *Proechimys* (Heteropsomyinae) and *Echimys* (Echimyinae) to be "myologically more different from each other than would be expected if these genera were in the same subfamily." To judge from Gorgas' descriptions and figures, *Cercomys* and *Proechimys* (Heteropsomyinae), *Kannabateomys* (Dactylomyinae) and *Echimys* (Echimyinae) do show certain differences each from the others in stomach structure, but a larger representation is obviously needed. As indicated above (p. 394), we have transferred *Chaetomys* from the Erethizontidae to be a subfamily of the Echimyidae because of its retention throughout life of dm_4^4, a characteristic of later echimyids and otherwise (now that we have made this transfer of *Chaetomys*) unknown among the Caviomorpha.

Our knowledge of fossil capromyines has been limited to Recent or sub-Recent material. The description of a number of new subgenera and species of capromyines from Cuba (Varona and Arredondo, 1979) brings the record of this group in the Pleistocene or Recent of Cuba to 8 genera or subgenera and 19 species, which suggests that the capromyines were of considerable importance in the Antillean fauna before the arrival of man, and strengthens the possibility that they had been there for a considerable time. Rodriguez *et al.* (1979) have discussed the Cuban capromyine (capromyid in their terminology) genus or subgenus *Mesocapromys* as a capromyine whose numerous primitive, echimyid-like features demonstrate the derivation of the capromyines from the echimyids. We accept their identification of the significance of this form as a primitive capromyine, and believe that this reinforces our opinion that the capromyines deserve only subfamilial status.

Following Patterson and Pascual (1972: Fig. 12) we place the Ctenomyidae (as a subfamily) in the Octodontidae.

The "classical" cavioid families, Caviidae and Hydrochoeridae, differ sharply from other hystricognaths in being superficially non-hystricognathous, the angle leaving the ramus close to the plane of the incisor. The masseteric crest is high on the jaw and heavily built, with a deep groove extending back to the vicinity of the condyle between the crest and the side of the ramus; the crest does not reach the angle, the insertions of parts of the masseter in that region being marked only by faint ridges. The lower incisor is short, ending under M_2. On the basis of these distinctive features some authors (e.g., Miller and Gidley, 1918; Ellerman, 1940) have separated the hystricognaths into two grand divisions, one for these two families and another for all the rest. This, of course, was going too far; cavies and capybaras are specialized in these respects. The extinct and broadly ancestral family Eocardiidae (Scott, 1905: 465) possessed a more normal hystricognath angle and a slighter masseteric crest that is lower on the side of the jaw and runs back and down to the angle. The shortened incisor, however, had been acquired by Deseadan time (Wood and Patterson, 1959: 371). Hartenberger (1975) suggested that the Hydrochoeridae deserve to be ranked as a superfamily,

largely on the basis of "*Villarroelomys*," which turned out not to be a hydrochoerid (p. 444). Capybaras clearly are good cavioids.

The principal uncertainties in caviomorph classification arise over the affinities of the Dasyproctidae, Dinomyidae and Cuniculidae. Are they cavioids, as Simpson and others maintained, or should they be placed elsewhere? The evidence advanced to support removal of dasyproctids, dinomyids and cuniculids from the Cavioidea was dental (Wood and Patterson, 1959: 324–329). All members of these families possess lower incisors of the usual length, and all of them have cheek teeth that differ in structure from those of cavioids *s.s.* Noting resemblances between the Deseadan chinchillid *Scotamys* and the contemporary dasyproctid *Cephalomys* in the structure of unworn or little worn molar crowns (the resemblances are real, no matter what interpretation one may wish to put upon them) and in general agreement with Schaub (*in* Stehlin and Schaub, 1951: 369–370), we transferred the families in question to the Chinchilloidea.

This proposal has of late met with less than universal approbation. Nearly all the new evidence is flatly against it. Gorgas (1967: 366–367) has found a close resemblance between the Cavioidea *s.s.* and the Dasyproctidae, etc., and decided differences between both and the Chinchillidae in stomach structure. Bugge (1971: 534) came to the same conclusion on the basis of the cephalic arterial system, as did Woods (1972: 190) for the muscular system and Vucetich (1975: 490) for the middle ear.

The evidence from chromosomes is interesting—and a little more complicated. George and Weir (1974: 90–93) distinguished four major groups of caviomorphs. One of them includes the Erethizontidae only, another the Octodontoidea. So far so good; it is in the composition of the other two that the surprise comes, especially in view of the virtually unanimous agreement reached—quite independently—by the other authors just mentioned. One of George and Weir's groups includes the Caviidae and Dasyproctidae, and the other the Cuniculidae, Hydrochoeridae and Chinchillidae (*Dinomys* was not available to them). They did, however, indicate (*op. cit.*: 100–101) a possible means of attaining (their Fig. 8) the *Hydrochoerus* and *Cuniculus* karyotypes "if it is assumed" that these forms "are cavioids with affinities with the Caviidae and Dasyproctidae respectively." We lay no claim to competence in karyology, but this possibility seems reasonable to us considering the weight of the other evidence.

Subjected to so heavy a barrage, we feel compelled to retreat and to replace the Dasyproctidae, Dinomyidae and Cuniculidae in the Cavioidea, although we admit to doing this without enthusiasm. Members of the group thus reunited agree in the total lack of a lateral process of the supraoccipital, in contrast to other caviomorphs, and most of them have a descending flange of the lacrimal, the dinomyids and *Cuniculus* lacking it. We wish to stress, however, that, within the Cavioidea as thus re-expanded, there is a split between the Dasyproctidae, Dinomyidae and Cuniculidae on the one hand and the Cavioidea *s.s.* on the other, and that this split occurred well prior to the Deseadan. We believe that this should be recognized in classification, and propose two subdivisions of the superfamily, that we call Series A and Series B (see below, p. 523). We offer no names for these subdivisions, since we consider the recent proposal by McKenna (1975a: esp. 40–42), according to which every identified stage in phyletic branching deserves special taxonomic status and a special name, to be a frightening example of the *inflatio ad absurdum* of higher categories that must inevitably result if cladistic classification is unthinkingly pushed to its logical limits. For a comment on a very similar proposal

made nearly half a century ago, see Simpson, 1945: 25–26, footnote 4.

The position of the Antillean Heptaxodontidae, usually grouped with the Dasyproctidae, Dinomyidae and Cuniculidae, is very uncertain. *Elasmodontomys* (of which *Heptaxodon* is a synonym) is not an echimyid, as are most West Indian genera, since it replaces dm_4[4] (Wood and Patterson, 1959: 326), as does *Amblyrhiza*. It possesses a very large lateral process of the supraoccipital, a structure absent even in rudimentary form in the families under discussion and also in all cavioids *s.s.* The cheek teeth are hypsodont, but not hypselodont, whereas in the Deseadan chinchillid *Scotamys* the rootless condition had already been achieved. Having thus been maneuvered, so to speak, into a corner, we end by offering the very unsatisfactory suggestion that in our present state of ignorance the family may best be listed as Caviomorpha *incertae sedis* as to superfamily.

Previously (1959: 321–322) we were skeptical as to the distinctness of the Family Perimyidae of Landry (1957: 55, 59), which he placed in the Chinchilloidea between the Cephalomyidae and Chinchillidae. Vucetich (1975), however, has brought forward evidence from middle ear structure that has convinced us of its distinctness, as a family related to the Chinchillidae. Other reasons for the acceptance of this group as a valid chinchilloid family were presented by Bondesio *et al.* (1975: 441–442). As pointed out by these authors, the family name, however, should be Neoepiblemidae, dating from Kraglievich, 1926. These now join the Chinchillidae, relieving the loneliness of their otherwise solitary splendor within their superfamily. The resemblances between *Cephalomys* and *Scotamys* in the cheek teeth suggest the possibility of a common ancestry for the Cavioidea and Chinchilloidea early in caviomorph differentiation.

To conclude this section, we mention a well known fact. The Deseadan fauna is isolated in time. It is separated from the one following, the Colhuehuapian, by perhaps 10 m.y., and it itself followed upon a hiatus in the record that surely lasted as long or longer. The ancestral caviomorphs arrived in South America during this hiatus—just when within it is not known, although we suspect near its beginning—but it is very clear that the rodents encountered in the Deseadan are at a not inconsiderable remove from the beginning of the caviomorph radiation. The initial burst, however, had not yet spent itself by the Deseadan. As a result, we encounter forms that are difficult to classify with assurance. We have done our best to indicate in the pages above and in our previous contributions such doubts and reservations as we have on these scores. We are reasonably sure that the systematic positions of *Platypittamys*, *Migraveramus*, *Deseadomys*, *Incamys*, *Scotamys*, *Asteromys*, *Chubutomys*, and *Protosteiromys* are as we have stated. We have presented the evidence for placing *Sallamys*, *Xylechimys*, *Cephalomys*, *Litodontomys*, and *Branisamys*, but we realize that there is room for discussion concerning them, as by Lavocat (1976: 72–73). We agree with him that much is indeed "provisoire." Hoffstetter (1976: 8) has stated that "la classification des Caviomorphes, et surtout celle des formes anté-Miocènes, demande une révision d'ensemble." Presumably he was referring to classification at higher rather than lower taxonomic levels. Better material of the Deseadan forms will help here to some extent, but we suspect that even if we knew all of them from complete skeletons, problems might still remain. What is needed is the filling of the hiatuses so that lineages can be traced rather than inferred.

Other Taxonomic Problems of the Hystricognathi

(1) *General* (by A.E.W.). One of the difficulties in trying to reach an accept-

able classification of the hystricognathous rodents is that, in our opinion, a number of authors shift between talking about hystricomorphs and hystricognaths as they go along, as though these two terms were synonymous. Recently, this approach seems to have been adopted by Lavocat (1978: 85). The hystricognathous rodents are those in which the angular process of the lower jaw arises from the lateral surface of the alveolus of the lower incisor. The hystricomorphous ones are those in which the origin of *M. masseter medialis* has spread forward through the infraorbital foramen to arise from the snout, resulting in great enlargement of the infraorbital foramen. These two features are *not* universally associated. There are sciurognathous hystricomorphs (Anomaluridae, Ctenodactylidae, Dipodoidea, Pedetidae and Theridomyoidea) as well as protrogomorphous hystricognaths (Bathyergidae, Tsaganomyidae, Cylindrodontidae, many reithroparamyids). *There is no possible way that the two of these features can be considered as both being always associated in a single rodent taxon and neither ever being present anywhere else.* As stated elsewhere (Wood, 1980c: 270), hystricognathy in rodents began to appear in the late Paleocene, and became gradually more fully developed. No trace of hystricomorphy is known before the middle Eocene (Theridomyoidea: Wood, 1974b: Fig. 4; Ctenodactylidae: Shevyreva, 1972b: 134–135, Fig. 1; 1976: Figs. 4–5, Pl. 1, Fig. 3b; *Prolapsus*: unpublished data).

As an illustration of this confusion of hystricognathy and hystricomorphy, we may quote Lavocat (1969: 1497) who stated that "Du point de vue systématique, nos conclusions confirment et complètent l'intuition fondamentale de Brandt en montrant que le sous-ordre des Hystricomorphes est une véritable unité naturelle, fondée sur des relations phylétiques précises et étroites." Aside from the fact that the "intuition fondamentale" should be credited to Waterhouse, 1839, rather than to Brandt, 1855 (who merely gave names to the groups that Waterhouse had identified), we believe that this statement by Lavocat is in complete contradiction of a vast amount of evidence. No return to the classification as proposed by Brandt is possible. One may assume that all the hystricomorphous forms are related, or that all the hystricognathous ones are, or that only those forms that are both hystricomorphous and hystricognathous belong together. But a combination of all three is impossible. It is a fundamental requisite that, in talking about these complicated matters, all authors should be careful to use precisely defined terms.

(2) *Infraorder Franimorpha* (by A.E.W.). Members of the Infraorder Franimorpha, varying from incipiently to fully hystricognathous, are known from the late Paleocene to early Oligocene (and possibly late Oligocene—Wood, 1980b: Table 1) of western United States and the late Eocene and earliest Oligocene of Mexico (Ferrusquía, 1978: 206). We believe them to have reached Asia at an unknown time or times during the Eocene (probably both early and late Eocene; see above, p. 449). Recent work (Wood, 1980b: 6; 1981: 86) has indicated that the North American Eocene-Oligocene Family Cylindrodontidae (represented in Central Asia, according to the classification we present here, by the Oligocene genera *Pseudocylindrodon* and *Morosomys* and by the Eocene to Oligocene *Ardynomys*) were at least subhystricognathous and hence were franimorphs.

The basic members of the infraorder are the rodents united by Wood (1962a: 117–118) as the subfamily Reithroparamyinae of the Family Paramyidae. As he pointed out (1962a: 117), the reithroparamyines were subhystricognathous; at least one genus (*Rapamys*; Wood, 1962a: 148) seems to have had an enlarged infraorbital foramen. Dawson (1977: 197,

n.) has queried the justification of calling the Reithroparamyinae subhystricognathous, saying "The 'very incipient' hystricognathous condition of *Reithroparamys* (Wood, 1973, p. 30–31) seems to me to be still a sciurognathous jaw, 'incipient' only *a posteriori*." This may be true, although the hystricognathy of *Reithroparamys huerfanensis* is quite well developed (Wood, 1962a: Fig. 46B), but as pointed out elsewhere (Wood, 1980c: 270) it is inconceivable that hystricognathy appeared instantaneously; it must have developed gradually, and the forms in which it was developing deserve to be called subhystricognathous or incipiently hystricognathous. Current taxonomic usage would seem to require them to be placed in the Suborder Hystricognathi.

The Franimorpha may be defined (modified from Wood, 1975b: 79) as: subhystricognathous to hystricognathous; protrogomorphous to hystricomorphous; with or without a distinct interparietal; alisphenoid does not extend much if any above level of glenoid cavity; at least sometimes a post-condyloid process on the mandible indicating the differentiation of the *M. masseter lateralis profundus, pars posterior*, deep division; molars cuspidate or crested, never a mesocone or mesoloph, sometimes a mesoconid but rarely a mesolophid; normal replacement of deciduous molars; and incisor enamel pauciserial or transitional from pauciserial to multiserial.

When Wood (1975b: 78–79) erected the Franimorpha, he placed the Reithroparamyinae in it, but left the other subfamilies of the Paramyidae in the sciurognath Infraorder Protrogomorpha, and left the Reithroparamyinae in the Paramyidae, which thus straddled the boundary between the two suborders. Wood still likes this idea—it indicates that the earliest known sciurognaths and hystricognaths were very closely related, but that they had already started to diverge in directions that would ultimately lead to such differences that their descendants were clearly very distinct from each other. Certainly no taxonomist living in Eocene time would have separated them at a level higher than that of subfamilies. Such a solution, of course, does not make for a neat set of cubby-holes. Patterson has now persuaded Wood that, although this is perhaps reasonable, it would not be generally acceptable.

We therefore recognize the Reithroparamyidae as a distinct family, that we define as follows: franimorphs with incipient hystricognathy; protrogomorphous in earlier and best known forms, infraorbital foramen enlarging in at least some later genera; bulla not co-ossified with the skull in earliest forms, but large and fused to the skull by middle Eocene; coronoid processes large and high; post-condylar process present at least sometimes; cheek teeth relatively simple, primitively tritubercular but with a distinct hypocone in upper molars and usually in P^4; metalophid incomplete, trigonid basin opening posteriorly; entoconid separated from posterolophid; transverse crest from entoconid toward hypoconid developing progressively, ultimately becoming a complete hypolophid; posterolophid progressively angulate at point of attachment to hypoconid; incisors narrow and compressed, enamel thin; skeleton, in the two cases where it is known, with elongate hind legs; size small to medium.

Guanajuatomys from the later Eocene of Mexico, and *Prolapsus* from the mid-Eocene of the Big Bend area of Texas, are both fully hystricognathous. *Prolapsus*, at least, had an enlarged infraorbital foramen. Both have been described, so far, on fragmentary materials. For both, better but undescribed materials are now available. The cheek teeth do not indicate close relationships between the two, or between either and any other well known group. We suspect that they belong to one or more Middle American franimorph families, but we know of no justification for the erection of such a family or families at the present time.

(3) *Cylindrodontidae and Tsagano-*

myidae (by A.E.W.). The Cylindrodontidae have long been recognized as a protrogomorph family, but the angular processes have been broken off from all described material. Recently a specimen was found that clearly had a hystricognathous angle and a small post-condyloid process (Wood, 1981: 86; in press a), which had led to the transfer of the family from the Protrogomorpha to the Franimorpha. The range of the family is middle Eocene (Bridger and Big Bend of Texas) through early Oligocene (Chadronian) and possibly late Oligocene of western United States, early Oligocene of Canada, earliest Oligocene of Mexico (Wood, 1980b: 6), as well as late Eocene and early (Ardyn Obo) and middle (Tatal Gol) Oligocene of central Asia. The incisor enamel was pauciserial in middle Eocene specimens of *Mysops* (Wahlert, 1968: 15), but uniserial in the early Oligocene *Cylindrodon* (*op. cit.*: 15).

Hussain *et al.* (1978: 101) suggested that the Chapattimyidae, from the middle Eocene of Pakistan, were ancestral, through *Petrokozlovia* of the middle to upper Eocene of central Asia (Shevyreva, 1976: 31) to the middle Eocene and later cylindrodonts of North America. This seems, on the face of it, most improbable. The tooth pattern of the Chapattimyidae does not suggest to me any affinities with later rodents other than the Ctenodactylidae. Structurally, the teeth of *Chapattimys* and *Saykanomys* from Pakistan (Hussain *et al.*, 1978: Pls. 1–6) are distinctly more advanced in their patterns than those of *Mysops* (Wood, 1973: Figs. 3, 4), as seems also to be true of *Petrokozlovia* (Shevyreva, 1976: Fig. 6). As indicated above (p. 504), the incisor enamel of the Chapattimyidae is pauciserial, which would allow them to occupy any position one wished.

For many years, Wood has argued (1937: 199; 1955: 171; 1970a: 17; 1974a: 50–53), in accord with the suggestion by Burke (1935: 3–4), that the cylindrodonts were ancestral, through the Asiatic *Ardynomys*, to the Mongolian genera *Tsaganomys*, *Cyclomylus* and their relatives. This view was accepted by Simpson (1945: 213), Wilson (1949: 93) and Schaub (1958: 1537). These genera were originally referred to the Bathyergidae (Matthew and Granger, 1923: 4; Teilhard de Chardin, 1926: 29–30), an assignment with which Landry (1957: 72–73) concurred. We here refer them to a distinct family, the Tsaganomyidae, related to both the Cylindrodontidae and the Bathyergidae.

There are many features in common between the cylindrodonts and the tsaganomyids, including both tooth and skull characteristics (Wood, 1974a: 51–52). The teeth of both are clearly four-crested in both upper and lower jaws, with no suggestions of any possible fifth crest or of a mesocone or mesoconid. The skull of the American species of *Ardynomys* (it is unknown in the Asiatic species) shows, among other features, a backward movement of the growing base of the upper incisor, so that it protrudes into the orbit in exactly the same area (although not not quite so far) and in the same manner as in the Tsaganomyidae. The arrangement in *Ardynomys* could probably also have given rise to the condition in the bathyergids, by an increase in the radius of curvature of the upper incisor, that would have pushed the growing base of the incisor upward and backward, so that it would have been enabled to grow backward. In the Tsaganomyidae, however, the upper incisor has extended its growing base back in the direction that had already been established in *Ardynomys*, as a result of which the large ridge, marking the course of the incisor across the anterior part of the orbit, forms a pronounced knob, lateral to M^{1-2}. There is much individual variation in the extent of this knob; sometimes there is an appreciable space below it above the alveolar border; in other specimens, the posteroventral end of the knob lies ventral to the occlusal surface of the upper cheek teeth. In these latter cases,

the ridge impinged on the course of the infraorbital artery, vein and nerve to the infraorbital foramen; we are not sure, but presume that they passed lateral to the incisive ridge.

We are informed by Dr. J. H. Wahlert (*in lit.*, 15 March 1980) "that the enamel of both *Cyclomylus* and *Tsaganomys* is intermediate between pauciserial and multiserial. *Cyclomylus* is closer to pauciserial and *Tsaganomys* to multiserial." Later, he added (*in lit.*, 28 March 1980) "The incisor enamel of *Mysops* .... is pauciserial with a slight inclination and is very much like that of *Cyclomylus*. Relationship is allowed but certainly not demonstrated by this similarity."

We define the Tsaganomyidae as follows: protrogomorphous and hystricognathous rodents of large size; skull massive; occiput forwardly sloping, very wide; bulla flattened anteriorly; zygomatic arch extending posteriorly well beyond posterior root of zygoma; incisors procumbent, presenting nearly straight forward as in specialized bathyergids; upper incisors extending back into orbit, bases forming bulges on side of maxillae, sometimes ending lateral and ventral to occlusal surface of M^{1-2}; lower incisors extending back to beneath condyles; incisor enamel transitional from uniserial to multiserial; cheek teeth hypselodont, four-crested; deciduous teeth replaced in normal manner, dm^3 small, peg-like, dm_4 essentially molariform; numerous burrowing adaptations in skeleton and body musculature.

Genera. Tsaganomys, Cyclomylus, Pseudotsaganomys if not a synonym of *Cyclomylus* (Kowalski, 1974: 159), *Sepulkomys* and *Beatomus* if valid.

Distribution. Middle to late Oligocene, Central Asia.

(4) *Bathyergidae.* In the Bathyergidae, the elongation of the upper incisors has carried the growing base nearly straight backward. The incisors of *Bathyergoides* (Lavocat, 1973: Pl. 7, Fig. 5) and *Proheliophobius* (Lavocat, 1973: Pl. 5, Fig. 6) make ridges part way across the orbit, directed about as in *Ardynomys* and *Bathyergus*. In the other bathyergid genera (*Cryptomys, Georychus* and *Heliophobius*) the growing base lies posterior to M^3. We do not believe that it would be possible to evolve the structure of the advanced Bathyergidae from that of *Tsaganomys*, or vice versa, although both could be derived from that of *Ardynomys*.

One of us (A.E.W.) believes that the franimorph family Cylindrodontidae was directly ancestral to the Tsaganomyidae and, probably, also to the Bathyergidae, although the Oligocene cylindrodonts are clearly too specialized to be bathyergoid ancestors, in that they had acquired uniserial incisor enamel. However, "*Cyclomylus* has inclined pauciserial enamel that looks a lot like [that of] *Mysops* but is thicker" (Wahlert, *in lit.*, 13 February 1980).

At the time of Patterson's death, we had not completely agreed on how we wanted to treat the cylindrodonts and tsaganomyids. At least at one time, Patterson felt that a relationship such as that described above would require the transferral of the Cylindrodontidae from the Franimorpha to the Bathyergoidea. Wood objected, because the Bathyergoidea are fully hystricognathous and have a pterygoid fossa that opens into the orbitotemporal fossa, whereas the cylindrodonts are subhystricognathous with a closed pterygoid fossa. The classification given below (p. 572) follows Wood's opinion.

Stromer (1923: 263; 1926: 134) described *Bathyergoides neotertiarius* from the Miocene of Southwest Africa (Namibia) and indicated that it was a definite bathyergid. He implied, although he was not certain (1926: 148), that it was involved in the ancestry of the Bathyergidae. Lavocat (1973: 109), in his description of the East African Miocene rodents, gave the date of publication of *Bathyergoides neotertiarius* as Stromer, 1924, a paper that he did not include in his bib-

liography. Both Stromer (1926) and Romer *et al.* (1962: 1341) give the date of publication of the paper in question as 1923, a figure that we accept.

Lavocat (1973: 109–133) also adopted the view that *Bathyergoides* was ancestral, at least structurally, to the Bathyergidae. He (1973: 150–153) made a case for considering that *Bathyergoides* was an intermediate stage between the thryonomyoids and the bathyergids, but we believe that the evidence of probable relationships of the bathyergids to the Oligocene tsaganomyids and of the latter to the Cylindrodontidae, rules out that possibility. As noted above (p. 473), if nematode evidence is of any value in rodent taxonomy, it should be a strong support for the absence of relationship between the bathyergids and thryonomyoids. It is also significant in this connection that the bathyergids and tsaganomyids are all protrogomorphous, with no forward extension of *M. masseter medialis*, except in *Bathyergoides* and, perhaps, in *Cryptomys*. Tullberg (1899: Pl. 2, Fig. 17), cited by Lavocat (1973: 151) as conclusive support for the existence of hystricomorphy in bathyergids, shows the jaw muscles of *Cryptomys* (cited as *Georychus*) *coecutiens* with *M. masseter medialis* just visible in the lateral view of the infraorbital foramen. Comparison of Tullberg's lateral view of the cleaned skull (1899: Pl. 2, Fig. 14) with the figure of the jaw muscles (1899: Pl. 2, Fig. 17) suggests that the muscle was merely visible through the infraorbital foramen, and that there was no actual penetration—in other words, no origin of any of the fibers from the snout in front of the foramen. However, in his text, Tullberg states (1899: 79) that a difference of this form from *Georychus capensis* is "... dass Foramen infraorbitale ... bedeutend weiter ist, als bei jener Art, und dass ein kleiner Teil des Masseter medialis ... dieses Foramen hier in der That durchsetzt."

Lavocat's figure of the skull of *Bathyergoides* (1973: Pl. 7, Fig. 5) shows the fossa of origin of *M. masseter medialis* lying in front of, but largely above, the infraorbital foramen. The direction of the fibers of the muscle must have been nearly vertical throughout, rather different from the condition in the other hystricognaths. We interpret these conditions to mean that there has been significant selective pressure acting on the Bathyergidae to lengthen *M. masseter medialis*, but that true hystricomorphy has never been generally attained in this family.

Lavocat has demonstrated (1973: Pl. 23, Fig. 2; Pl. 26, Figs. 1, 6; Pl. 29, Figs. 1–9; Pl. 30, Figs. 1–6) that the cheek teeth of *Bathyergoides* (and probably of other bathyergids) are based on four transverse crests, with no trace of mesoloph or mesolophid (Fig. 30K), as is also true in the Tsaganomyidae. We have been unable to determine, either from Lavocat's description or from his pictures, whether there was normal replacement of the deciduous teeth or whether they were retained. It seems clear that the anterior tooth of the series generally had the same pattern as the subsequent teeth (Lavocat, 1973: Pl. 26, Fig. 1; Pl. 29, Figs. 1, 7; Pl. 30, Figs. 1, 2, 5), which suggests that they were P_4^4 rather than dm_4^4. There clearly was rapid wear of the cheek teeth, so that one tooth was considerably worn before the one behind it came into use. This, of course, is normal among burrowing rodents.

Lavocat has suggested (1973: 109, 122, 123) that there were four upper and five lower cheek teeth in *Bathyergoides*. This latter number was based on the jaw of no. SO 736, which has three cheek teeth in use, a fourth that had not as yet erupted, and what Lavocat identified as an alveolus at the front of the series (1973: Pl. 30, Fig. 4). We are somewhat hesitant in accepting four upper and five lower cheek teeth as being the correct formula for *Bathyergoides*, as it would be unique among rodents.

The whole matter of what teeth are present in bathyergids is still unsettled, but it is extraordinarily unlikely that P_3 is one of them (Lavocat, 1973: 123), since this tooth is otherwise unknown among the Rodentia. It seems probable that the increase of the cheek-tooth formula of bathyergids (up to $_6^6$) involves either the retention of dm_4^4 along with P_4^4, or the duplication of one or more teeth as in *Otocyon* (Wood and Wood, 1933: 43), or both. Certainly, if *Bathyergoides* possesses P_3, it could not have been descended from any known or reasonably anticipated Eocene or Oligocene rodent.

It seems improbable to us that the Bathyergidae secondarily became protrogomorphous, as Lavocat (1973: 151) proposed. We know of no cases where such a secondary development has been demonstrated. If, as seems clear, the forward growth of the origins of the branches of the masseter was an adaptation that increased the functional strength of the muscles that moved the incisors, it would be most amazing to find a secondary reduction of the jaw muscles in animals that had highly modified the incisors to permit their extensive use in burrowing. Such a reduction would have been much more remarkable than the retention of the primitive protrogomorphous condition by rodents that might have been helped had they evolved modified jaw muscles. The retention of protrogomorphy would simply mean that (as in the case of *Aplodontia*) the pertinent mutations had not occurred under the proper conditions. Reversion to protrogomorphy would require not only the reverse mutations, but also selection for less efficient jaw muscles.

All the features discussed above seem to us to demonstrate that the Bathyergidae could not have been descended from the Thryonomyoidea as Lavocat believed, and as Wood was once willing to accept (1975b: 942). We agree with the conclusions of Hill *et al.* (1957: 511) that the available data "point . . . emphatically towards a complete severance of the bathyergids from all" other living rodents.

Bathyergoides apparently was a primitive member of the Oligocene stock from which the Bathyergidae were derived, but was on a side line as shown by the fact that it had begun to develop hystricomorphy. Although we are not certain of the precise relationships of *Bathyergoides*, we see no valid reason for separating it from the Bathyergidae. The definition of the Family Bathyergoididae, as given by Lavocat (1973: 109)—"Famille de Bathyergoidea dans laquelle la structure des dents jugales est bien conservée."—is perhaps a valid generic diagnosis, but hardly seems worthy of familial separation.

We therefore define the Bathyergidae as follows: protrogomorphous to occasionally slightly hystricomorphous hystricognaths; skull and skeleton highly modified for burrowing; occiput broad, inclined forward; incisors hypertrophied and procumbent, with growing bases extended unusually far to the rear; cheek-tooth formula variable, with additional teeth of unknown nature; cheek teeth hypsodont to hypselodont, with crown patterns based on four transverse crests in both upper and lower teeth, with no trace of mesoloph or mesolophid; incisor enamel multiserial.

As we have tried to indicate, there are many similarities between the Tsaganomyidae and the Bathyergidae, as well as differences. It seems probable, however, that the two are related, both being descended from late Eocene or early Oligocene Asian cylindrodonts (but *not* from chapattimyids). We therefore unite the two families in a Superfamily Bathyergoidea. We have no feelings as to whether one or two lines crossed the boundary from the cylindrodonts to the Bathyergoidea.

(5) *Hystricidae*. Lavocat (1973: 160) included the Hystricidae, together with the Bathyergoidea and the Thryonomyoidea,

in his Infraorder Phiomorpha, and believed the common ancestry of all to have been primitive thryonomyoids. He stated (1969: 1496) that some East African forms "correspondaient parfaitement à ce que l'on pouvait attendre" of hystricid ancestors, but neither at this time nor later (1973: 153–158) was he more specific nor did he demonstrate how the hystricids could possibly be descended from anything that had begun to acquire the features that characterize the Thryonomyoidea. Lavocat noted (1978: 74), for the first time so far as we are aware, that, in the Hystricidae, there is "replacement of dP^4 by P^4," without apparently realizing that this makes all known thryonomyoids too advanced to be hystricid ancestors. Incidentally, it should be emphasized that, in the hystricids (in contrast to all known thryonomyoids) there is also universal replacement of dm_4 (dP_4) by P_4 at the ontogenetic stage normal for mammals.

As pointed out elsewhere (Wood and Patterson, 1970: 632–633; Wood, 1974b: 38) derivation of hystricids from Oligocene or later thryonomyoids is impossible, because all hystricids have a normal mammalian replacement of the deciduous teeth. The reverse direction, derivation of thryonomyoids from Eocene hystricids, would be possible, although we know of no evidence in support of such a derivation. Since no hystricids are known before the late Miocene, one can use one's imagination rather freely in determining the characteristics of Eocene hystricids. Lavocat (1978: 79) stated that "There does not exist in the lower Miocene of Africa any known form which could be said with certainty to be ancestral to the Hystricidae . . . ." In fact, one can go farther, and state with complete confidence that all known Oligocene and early Miocene African rodents can be completely ruled out as possible ancestors of the Hystricidae.

Where the hystricids lived in the mid-Tertiary and from what they were derived are pure guesses. Our guess would be that they lived in southern Asia, and that they were derived from the same hypothetical franimorph population that we believe to have been ancestral to the thryonomyoids. It is clear to us that there are no known rodents that could be considered to have been immediately ancestral to the Hystricidae.

If Lavocat was correct that the Hystricidae and the Thryonomyoidea should be united at the infraordinal level, the term "Hystricomorpha" ought to be used for the combination, since it has both long priority and very general acceptance. Lavocat's concept, "Phiomorpha," is essentially identical to the concept "Hystricomorpha" of those authors who are willing to accept the Caviomorpha as a distinct entity. The general acceptance of the term "Hystricomorpha," even when it is used in no more modern a sense than that of Brandt (1855) was shown by its usage, by all who were not taxonomists, at the symposium on the Hystricomorpha, held in London in 1973 (Rowlands and Weir, 1974).

We here consider the Infraorder Hystricomorpha to include, for the time being, only the Family Hystricidae. We believe that future discoveries will not demonstrate that the Bathyergoidea belong here. We have no opinion as to whether it will be shown that the hystricids and the thryonomyoids had a common ancestor that had evolved beyond the franimorph stage. If they did, they should be united in the Hystricomorpha; if not, the term Phiomorpha may be retained for the Thryonomyoidea.

(6) *Thryonomyoidea.* As indicated, we here restrict the Infraorder Phiomorpha to the Thryonomyoidea. Throughout this paper, we have used the latter term to avoid confusion, since our usage of "Phiomorpha" is so different from that of Lavocat. It is perhaps not necessary to retain three infraorders (Bathyergomorpha, Hystricomorpha and Phiomorpha) for the Old World Hystricognathi, but

this at least would emphasize our current complete ignorance of the interrelationships of these groups. It may even have been the case that the Eocene franimorph ancestors of the caviomorphs and thryonomyoids were more closely allied to each other than either was to the ancestors of the Hystricidae and Bathyergoidea.

It is perhaps presumptuous on our part to differ with Lavocat on the classification of the Thryonomyoidea, but there are a number of points on which we have come to differ with his conclusions, and we believe that we should present these and explain our reasoning.

We do not believe that *Thryonomys* and *Petromus* should be united in a single family, since we believe (as apparently Lavocat did likewise) that they belong to lines that were already separate in the lowest levels of the Jebel el Qatrani Formation. Wood (1968: 68–73) compared *Gaudeamus* with *Thryonomys*, and pointed out many similarities in tooth and jaw structure (cf. Wood, 1968: Figs. 14–15 and Wood, 1962b: 317–320, Fig. 2A–C); Wood's phylogenetic chart (1968: Fig. 17) showed *Gaudeamus* as approximately ancestral to *Thryonomys*. Lavocat (1973: 162) considered *Gaudeamus* as much too specialized to occupy such a position, although he kept the two together in the Thryonomyinae. We see no evidence of such precocious specialization, and believe that *Gaudeamus* was very close to, if not actually, the ancestor of *Thryonomys*. We believe that these genera belong to a group that early acquired highly crested cheek teeth, with the crests reduced essentially to three in all teeth except dm_4 (Wood, 1962b: Fig. 2A–B).

We do not believe that *Neosciuromys africanus* Stromer is a synonym of *Paraphiomys pigotti*, since *Neosciuromys* clearly had higher crowned teeth than *Paraphiomys* and had reduced the pattern of the lower cheek teeth to three transverse crests with no trace of subsidiary elements (Fig. 30G), whereas in *Paraphiomys pigotti* and *P. stromeri* (Lavocat, 1973: Pl. 26, Figs. 7–10; Pl. 27, Figs. 3–4, 9–10; Pl. 28, Figs. 6–7) the teeth are very brachyodont and there are always elements of the metalophulid II present.

In his table of tooth measurements (1973: 272, Table 14), Lavocat gives no measurements of lower teeth of *Paraphiomys pigotti* except one of 15.0 for what we believe is the length of the tooth row. He gives lengths of individual teeth of three specimens of *Paraphiomys stromeri* (including the type); these suggest that, in the latter species, the teeth are about 2 mm long. The lengths of the lower cheek teeth in Stromer's three specimens of *Neosciuromys africanus* range from 3.40 to 4.48 mm, so that they would seem to be appreciably larger than those of *Paraphiomys pigotti*. Finally, in *Neosciuromys*, M_2 is significantly larger than any of the other cheek teeth (Fig. 30G). *Neosciuromys* clearly was a member of the Thryonomyidae.

The specimen from the Jebel el Qatrani Formation of Egypt, described by Wood (1968: 48–51, Fig. 5F) as *Paraphiomys simonsi*, agrees with *Neosciuromys africanus* in the simplification of its pattern (although it has not gone quite so far), in its appreciable height of crown, and in the large size of M_2 (and M_3). There seems no basis, now that illustrations of all the Miocene forms are available (which they were not when Wood's 1968 paper was written) for not including this species in *Neosciuromys* as *N. simonsi*, a species somewhat smaller and more primitive than the early Miocene *N. africanus*.

Lavocat (1973: 21) defined the subfamily Thryonomyinae (=our Thryonomyidae) simply as "Thryonomyidae dont la structure des dents jugales n'est pas trés simplifiée." On the contrary, we believe, these forms clearly have very simplified tooth patterns, at least in comparison to the other Oligocene and Miocene thryonomyoid genera.

Petromus (Wood, 1962b: Fig. 1C–F)

has a very different tooth pattern from that of the Thryonomyidae, it being based on four transverse crests rather than three. This type of pattern is found in a considerable number of the Oligocene and Miocene African genera. The oldest family name available for these is Petromuridae of Tullberg, 1899 (as Petromyidae). We divide these, in general following Lavocat's opinions of the relationships of the various forms, but not his formal taxonomy (1973: 160), into three subfamilies: the Phiomyinae to include *Phiomys*, *Paraphiomys*, *Kenyamys*, *Simonimys* and *Epiphiomys*; the Diamantomyinae (we can see no justification for considering these a separate family) for *Metaphiomys* (Fig. 30E), *Diamantomys* (Fig. 30J) and *Pomonomys* (Fig. 30H–I); and the Petromurinae for *Petromus*. Lavocat placed *Metaphiomys* in a separate subfamily from the Miocene genera that he recognized (1973: 52, 160) as its probable descendants; this seems unwarranted to us, and we agree with his statement in the descriptive part of his paper (1973: 71) that he felt he should adopt a vertical classification and consider *Metaphiomys* the direct ancestor of *Diamantomys* and *Pomonomys*.

Lavocat's Family Myophiomyidae unites all the highly cuspidate genera, but it may not be a natural group. *Phiocricetomys* differs widely from the others in the very large size of the cingulum and the length of the anterior tooth, in the roundness of the individual cusps, and in the reduction of the dentition in the only known specimen to three cheek teeth (Wood, 1968: Fig. 16). Wood (1968: 74–75) concluded that the teeth were more probably M_{1-3} than dm_4–M_2; however (p. 496), perhaps they are dm_4–M_2. The apparent reduction of M_3 in *Elmerimys* (Lavocat, 1973: 105; Pl. 28, Fig. 11) could be a clue pointing in the same direction, if Lavocat's two subfamilies (Phiocricetomyinae and Myophiomyinae) really belong together. It is clear from Lavocat's text (1973: 103, 108) that he intended to include *Phiomyoides* in the Myophiomyinae, but that it was inadvertently omitted from his table on page 160. We believe that *Andrewsimys* also belongs here, on the basis of Lavocat's definition of the family, rather than in the Phiomyinae where he placed it. For the present, but with great uncertainty, we accept the union of Lavocat's Subfamilies Phiocricetomyinae and Myophiomyinae in the Family Myophiomyidae.

Lavocat (1973: 163) reported the discovery, in the Eocene of Pakistan, of an undescribed genus, which he suspected "puisse avoir déjà présenté toutes les structures essentielles des Phiomorpha . . . ." This citation was quoted by Wood (1975a: 75–76, 78) as an occurrence of the Phiomorpha in the Eocene of Pakistan. Although we are not sure, we believe that this is probably a specimen of the material described by Hussain *et al.* (1978) as members of the Chapattimyidae, a group that we do not believe had anything to do with the ancestry either of the Thryonomyoidea or of the Hystricidae. As those authors noted (Hussain *et al.*, 1978: 75), the only rodents they refer to this family whose lower jaws are known were sciurognathous. These seem most unlikely ancestors for the thryonomyoids. Lavocat has informed Wood (*in lit.*, 25 Jan. 1979) that he no longer believed "que les Rongeurs de l'Eocéne du Pakistan soient apparentés aux Phiomorphes. . . . ces Rongeurs ont tous un *très fort* mètaconule, ce qui ne s'accorde pas du tout avec la structure de *Phiomys andrewsi*."

Recently, Shevyreva and Chkhikvadze (1978: 418) have suggested, in a brief abstract, that a form represented by a lower jaw ("Sp. 3") from the middle Eocene of Kazakhstan, might have something to do with the ancestry of the "Phiomorpha." We doubt whether any fossils yet reported have any bearing on the immediate ancestry of the thryonomyoids.

Lavocat (1973: 20) cited the Infraorder Phiomorpha as dating from Lavocat, 1967, but listed, in his Bibliography, two papers of that date, Lavocat 1967A and 1967B. In the former paper, which dis-

cussed the Miocene rodents of East Africa and their relationships, he neither used nor defined the term "Phiomorpha." The expression "Superfamille des Phiomyoïdés" was used on page 60, and the term "Phiomyoidae" [*sic*] in the abstract (1967a: 57). The second paper, discussing the ear region of the theridomyoids, used the terms "Phiomorphes" and "Phiomorphs" in the French and English abstracts, respectively (1967b: 491), and the text makes comparisons of the theridomyoid ear with that of "Phiomorphes," not otherwise identified, the term being used three times (1967b: 498).

The only attempts by Lavocat at a definition of the Infraorder that we have found were in his East African monograph (1973: 20), and in his chapter (1978: 71) on the Rodentia and Lagomorpha in "Evolution of African Mammals." In the first of these papers, his definition seems hardly adequate: "*Définition*: Rongeurs d'introduction ancienne en Afrique, de provenance actuellement inconnue, de distribution actuelle tropicale à tempéré chaud, dans l'Ancien Monde exclusivement. Structure infraorbitaire primitivement hystricomorphe, très modifiée et régressé dans la famille des Bathyergidae. 4 ou 5 dents jugales, ou plus chez certains Bathyergoidea." His later definition was more illuminating: "Infraorder Phiomorpha Lavocat 1962. DIAGNOSIS. Lower jaw always hystricognath. Infraorbital structure primarily hystricomorph, greatly modified and secondarily reduced in some Bathyergoidea. Molar teeth morphologically tetra- or pentalophodont; greatly simplified in the Bathyergidae. Generally four cheek teeth, rarely three, sometimes five" (1978: 71). Even this definition does not separate the "Phiomorpha" from the Caviomorpha.

Lavocat concluded his monumental work on the early Miocene rodents of East Africa with the remark that above all we now need rodent faunas from the Eocene of South America and Africa (1973: 258). We heartily agree, and add Middle America to the list, along with more extensive rodent faunas from the Eocene of both north and south Asia.

Classification of the Suborder Hystricognathi

We now summarize, in tabular form, our current ideas as to the classification of the Suborder Hystricognathi.

Suborder Hystricognathi Tullberg 1899
- Infraorder Franimorpha Wood 1975a
  - Family Reithroparamyidae (new rank; Wood, 1962a as a subfamily)
  - Family Protoptychidae Wood 1937
  - Family Cylindrodontidae Miller and Gidley 1918 (excluding the Subfamily Tsaganomyinae; otherwise as given by Wood, 1974a)
  - *Incertae sedis* as to family—*Guanajuatomys* and *Prolapsus*
- Infraorder Bathyergomorpha Roberts 1951
  - Superfamily Bathyergoidea Osborn 1910
    - Family Bathyergidae Waterhouse 1841 (Bathyergidae of authors, plus *Bathyergoides, Proheliophobius* and *Paracryptomys*, if the last is not a *nomen vanum*)
    - Family Tsaganomyidae Matthew and Granger 1923 (as a subfamily)
- Infraorder Hystricomorpha Brandt 1855 (as a suborder; Tullberg, 1899 as an Infraorder)
  - Family Hystricidae Burnett 1830
- Infraorder Phiomorpha Lavocat (first formal use as an infraorder by Lavocat, 1973: 20; first undefined use of the term "Phiomorphes" by Lavocat, 1967b: 491, 498; Lavocat, 1978: 71 dates the infraorder from Lavocat, 1962, in which paper neither "Phiomorpha" nor "phiomorphes" is used)

Superfamily Thryonomyoidea Wood 1955
Family Thryonomyidae Pocock 1922
Genera: *Gaudeamus, Neosciuromys, Thryonomys*
Family Petromuridae Tullberg 1899 (as Petromyidae)
Subfamily Petromurinae Ellerman 1940
Genus: *Petromus*
Subfamily Phiomyinae Schlosser 1911 (including Family Kenyamyidae Lavocat 1973)
Genera: *Phiomys, Paraphiomys, Kenyamys, Simonimys, Epiphiomys*
Subfamily Diamantomyinae Schaub 1958 (as a family; including Subfamily Metaphiomyinae Lavocat 1973)
Genera: *Metaphiomys, Diamantomys, Pomonomys*
Family Myophiomyidae Lavocat 1973
Subfamily Myophiomyinae Lavocat 1973
Genera: *Myophiomys, Elmerimys, Andrewsimys, Phiomyoides*
Subfamily Phiocricetomyinae Lavocat 1973
Genus: *Phiocricetomys*
Infraorder Caviomorpha Wood and Patterson 1955 (in Wood, 1955, as a suborder)
Superfamily Erethizontoidea Simpson 1945
Family Erethizontidae Thomas 1897 (Erethizontidae of authors less *Chaetomys*)
Superfamily Octodontoidea Simpson 1945
Family Octodontidae Waterhouse 1839 (including as a subfamily, Ctenomyidae Tate 1935)
Family Echimyidae Gray 1825 (as Echimyna)
Subfamily Echimyinae Murray 1866
Subfamily Adelphomyinae Patterson and Pascual 1968
Subfamily Dactylomyinae Tate 1935
Subfamily Chaetomyinae Thomas 1897
Subfamily Heteropsomyinae Anthony 1917
Subfamily Plagiodontinae Ellerman 1940 (as Plagiodontiinae)
Subfamily Capromyinae Smith 1842 (as a family)
Subfamily Myocastorinae Ameghino 1904 (as a family)
Family Abrocomidae Miller and Gidley 1918
Superfamily Cavioidea Kraglievich 1930b
Series A, new
Family Eocardiidae Ameghino 1891
Family Caviidae Waterhouse 1839
Family Hydrochoeridae Gill 1872
Series B, new
Family Dasyproctidae Smith 1842
Family Dinomyidae Alston 1876
Family Cuniculidae Miller and Gidley 1918
Superfamily Chinchilloidea Kraglievich 1940
Family Chinchillidae Bennett 1833
Family Neoepiblemidae Kraglievich 1926
Incertae sedis as to superfamily
Family Heptaxodontidae Miller and Gidley 1918

CONCLUSIONS (by A.E.W.)

The skulls, lower jaws and dentitions of rodents from the Deseadan Oligocene of Bolivia are described. *Migraveramus*

is referred to the Octodontidae, *Sallamys* to the Echimyidae, *Incamys* to the Dasyproctidae and *Branisamys* to the Dinomyidae. Two undescribed dasyproctid genera are briefly discussed, as well as material referred by Lavocat (1976: 59–62) to the Patagonian genus *Cephalomys*. It is concluded that the Bolivian genus *Luribayomys* and the Uruguayan genus *Palmiramys* are *nomina vana*.

The largest part of the paper is the discussion section. The two contemporary theories of the origin of the Caviomorpha, namely transatlantic transportation of African waif migrants or island hopping from Middle America directly or through the Antilles, are discussed. It is pointed out that, whichever hypothesis is accepted, there has been independent evolution of the Old and New World hystricognath rodents for at least the last 40 m.y.

During the Eocene, the Atlantic Ocean was narrower than at present. In the earliest Eocene, there was a high latitude North Atlantic connection between Europe and North America that enabled paramyid rodents from the latter to reach the former. Europe at this time was separated from Asia by a wide waterway (at least, there is no evidence that any mammals were able to cross this waterway in either direction). The waterway closed during the early Oligocene (the "grand coupure"), permitting the invasion of Europe by a wide variety of Asian mammals.

South Asia (Pakistan, India, southeastern Asia) had, quite certainly, attained its present relationship with northern Asia at least by the middle Eocene, from which time a very considerable fauna of terrestrial mammals, almost all of north Asiatic aspect, are known. The complete absence of any reported autochthonous terrestrial south Asiatic faunal elements, other than possible moeritheres, suggests rather strongly that these southern areas may have been part of the Asian continent for a considerable period of time.

The exact Eocene relationships between Asia and North America are not known. There almost certainly was a high-latitude land connection in the late Paleocene or early Eocene, that permitted the transfer of early Eocene rodents from one continent (we believe North America) to the other. There was also a connection later in the Eocene that permitted the Cylindrodontidae to reach Asia and the Lagomorpha to reach North America.

Africa had long been isolated from the rest of the world. The African Eocene mammalian fauna was largely different from that of any other part of the world, although species questionably referred to the Palaearctic genera *Apternodon* and *Brachyodus* are present (Simons, 1968: 15). By the end of the Eocene, as these two forms indicate, Africa had established sufficiently close relationships with Palaearctica (presumably through southwestern Asia) to have permitted a few invasions. These must have included the thryonomyoid rodents (still unknown from the Asian Eocene or Oligocene).

South America, like Africa, was an island continent during the Eocene. There had been a situation earlier that permitted some waif dispersal between North and South America, whether in one direction or both is uncertain. At some unknown time after the mid-Eocene Musters, caviomorph rodents reached South America. And, at some pre-Deseadan date probably later than the arrival of the rodents, primates reached South America.

Rodents that show the initial stages of the development of hystricognathy (the migration of the angular process a short distance laterad of the incisive alveolus) appear in the late Paleocene of western United States. These and their later but generally similar descendants are united in the Infraorder Franimorpha. Hystricognathy increases among North American rodents during the Eocene, being completely developed in the middle Eocene *Prolapsus* from Texas. Hystrico-

morphy also appears in a number of franimorph lines. Although hystricomorphy appears in middle Eocene theridomyoids of Europe and ctenodactylids of Asia, all evidence indicates that neither of these groups ever developed, or gave rise to forms that developed, hystricognathy.

The Eocene fauna of Middle America is very poorly known. But there were a number of hystricomorphous and hystricognathous lines of rodents evolving in this area. Among these are the rodents of the Family Cylindrodontidae, which were hystricognathous but protrogomorphous. We believe that Middle American members of this family were ideal candidates, both in their geographic location and their structural features, to have been the ancestors of the Caviomorpha.

The Eocene relationships of North and South America are poorly known. There would seem, however, to have been periods of orogeny, forming chains of volcanic islands more or less along the course of the present Isthmus of Panama, in the middle Eocene, and there was unquestionably a chain of islands connecting Middle America and South America along the course of the present Antilles. Either of these would have provided a much easier invasion route to South America than the South Atlantic would have.

The Deseadan rodent fauna was compared with that of present-day northeastern Brazil. The frequency make-up at the various localities is strikingly similar in the two cases, with (usually) one species per locality the predominant one, but with relative abundances varying widely from locality to locality, even between those in close proximity. Rodents are one of if not the most abundant order in all Deseadan localities that have produced extensive collections.

In contrast, the early Oligocene rodents of Africa are much less diverse, taxonomically, than are the South American ones. In nearly every collecting locality, they are both individually and by taxa much less abundant than was the case with the Deseadan rodents. The only exception (Yale Quarry G) was a small quarry, producing only small mammals; here there was an overwhelming preponderance of one species of rodent.

The African Oligocene rodents were contrasted with their contemporaries, the rodents of the Porvenir local fauna of the early Oligocene Chambers Tuff Formation of Trans-Pecos Texas. Here six families of rodents are present, one with 3 and two with 2 subfamilies each, 13 genera and 15 species, all represented by a total of 44 specimens. Obviously, the diversity of North American early Oligocene rodents was vastly greater than that of their African contemporaries (only two closely related families, 3 genera and 4 named species plus 2 possible additional ones, are represented among 59 specimens from the early Oligocene). This clearly disproves the hypothesis that rodents reached Africa in the Paleocene or early Eocene.

The early Miocene rodents of East Africa present a very different picture. Here the numbers and diversity of the rodents are very similar to those in the South American Deseadan. We feel that this very clearly indicates that, in the early Oligocene, rodents had been in South America about as long as, in the early Miocene, they had been in Africa. The East African rodents consist of two groups—the descendants of the Oligocene forms, and a group of very recent immigrants, presumably from southwestern Asia (Bathyergidae, Anomaluridae, Pedetidae, Cricetidae, Sciuridae). Although the latter group is represented by more taxa than are the thryonomyoids, they make up less than 10% of the individuals that have been collected, and were obviously just beginning to establish a foothold on the continent.

The Oligocene rodents of Africa are compared with the Recent murids of Australia. These last apparently reached that continent from the East Indies about 4.5

m.y.b.p., and have since diversified in a continent where they had no competitors. The morphologic diversification of the Australian Pseudomyinae seems somewhat greater than that of the African Oligocene thryonomyoids (separated into three families not because they are that different but because their Miocene descendants achieved greater diversity).

That is, rodents would seem to have reached Africa no more (and probably less) than 4.5 m.y. before the deposition of the lower fossil wood zone, but to have reached South America two or three times as much before the Deseadan. Allowing for the various uncertainties, this would indicate that rodents had reached Africa in the latest Eocene, but that they arrived in South America about the middle of the Eocene.

The evidence for a close relationship between the Caviomorpha and the Old World hystricognaths, based on parasitic nematodes, has been milked for all it is worth. There apparently has been as much parallelism among heligmosomid nematodes as Wood thinks there has been among rodents; the entire basis for heligmosomid support of relationship between thryonomyoids and caviomorphs is, apparently, based on the genus *Paraheligmonella*, present in certain echimyids. If we interpret her meaning correctly, Durette-Desset (1971: 50) was very uncertain as to the accuracy of her assignment of this genus to the otherwise exclusively Old World family Heligmosomidae.

The oxyurine nematode *Evaginuris* is primarily known from caviomorphs. Two species have been reported from *Hystrix*, but both records deserve to be questioned. In one case, the host was a zoo specimen that could have been infected from contact with an American porcupine. The other species might also have been in a zoo specimen, and, in addition, the author of the species seemed to question either the accuracy of the identification of the host or the association of the nematode with that host. In any case, *Evaginuris* is an exceedingly doubtful support for thryonomyoid-caviomorph relationships.

Similarities occur between the fleas and lice of Old World and New World hystricognaths (Traub, 1980). These, we believe, indicate that the caviomorphs and the Old World forms are more closely related to each other than either is to any other living rodent, but there seems to be just as much support from these pests for a North or Middle American origin of the caviomorphs as for an African one.

A detailed analysis was made of the morphologic features that have been cited by various authors, especially Lavocat (1973: 168) as indicative of close relationships between the Oligocene and later caviomorphs and the Old World hystricognaths, similarities supposedly so great as to require the rafting of thryonomyoids from Africa to South America. Hystricognathy is common to both groups, but is likewise present in the North American Eocene-Oligocene franimorphs. This feature developed to permit lengthening of *M. pterygoideus internus*. This lengthening also resulted in deepening and eventual perforation of the dorsal margin of the pterygoid fossa. Due to damage in all available specimens, it is not known whether or not such deepening and perforation had occurred in the Eocene franimorphs. Hystricognathy, certainly, could have been inherited by both thryonomyoids and caviomorphs from Holarctic franimorph ancestors.

Some features (structure of the middle ear, presence of an internal carotid artery, and serology) separate the Erethizontidae from all other post-Eocene hystricognaths. These features would seem to indicate that they are more primitive than any of the Thryonomyoidea, and would permit them to have given rise to the Old World forms (which we do not believe happened) but would seem to be a complete barrier to their being descendants of thryonomyoids.

The Bathyergoidea are similarly isolated from all other post-Eocene hystricognaths, because of their retention of protrogomorphy, their rather distinctive ear ossicles with much greater fusion than occurs in any other hystricognaths, their smooth brains and their distinctive nematodes.

A number of the features cited by Lavocat and Hoffstetter are not, as they implied, hystricognath characters, but are widely distributed among rodents in general.

We conclude that the evidence indicates that the Caviomorpha and Old World hystricognaths are related; that it is morphologically impossible for the Thryonomyoidea to have given rise to the Caviomorpha or to the Hystricidae, but that evolution in either of the reverse directions would have been possible; and that the most probable scenario is for both the Thryonomyoidea and the Caviomorpha to have been derived from middle Eocene northern hemisphere franimorphs, even though these are still unknown in the Old World.

A classification of the Suborder Hystricognathi is presented. Among the Caviomorpha, several changes are made from our 1959 classification. These involve: transferral of the Chaetomyinae and Capromyinae to the Echimyidae, and of the Ctenomyinae to the Octodontidae; transferral of the Dasyproctidae, Dinomyidae and Cuniculidae from the Chinchilloidea to the Cavioidea; division of the Cavioidea into two Series, one for these three families and the other for the Eocardiidae, Caviidae and Hydrochoeridae; transferral of the Heptaxodontidae out of all recognized superfamilies to become *incertae sedis*; and recognition of the Neoepiblemidae as a second family of chinchilloids.

Among the Franimorpha, the Reithroparamyidae are raised to family status, and the Cylindrodontidae are included because they have recently been discovered to have been hystricognathous. The northern Asiatic Tsaganomyidae are considered to have been descended from the cylindrodonts but to be bathyergoids rather than franimorphs. It is concluded that there are no relationships whatsoever between the rodents from Pakistan included in the Chapattimyidae by Hussain *et al.* (1978) and either the Thryonomyoidea or the Cylindrodontidae.

We doubt that the modern Bathyergidae are secondarily protrogomorphous, as Lavocat (1973: 151) has proposed, and consider that *Bathyergoides* was specialized, not primitive, in its possession of partial hystricomorphy. The totality of the evidence seems to us to show that the Bathyergoidea were of northern Asiatic origin, evolving from Oligocene cylindrodonts, and that they have no relationship (except descent from primitive franimorphs) with other hystricognaths.

There continues to be no information as to the ancestry of the Hystricidae. We have no opinion as to whether they were ancestral to the Thryonomyoidea or whether the two groups evolved independently from the Franimorpha. We feel certain that the hystricids are not descended from thryonomyoids.

If the Thryonomyoidea and Hystricidae are related at the infraordinal level, they should be united in an Infraorder Hystricomorpha rather than Phiomorpha, since the former term has long priority and essentially universal recognition.

We recognize three families of the Thryonomyoidea—the Thryonomyidae, Petromuridae and Myophiomyidae. In the first family we place *Thryonomys*, *Gaudeamus* and *Neosciuromys*, the last being quite distinct from *Paraphiomys* with which Lavocat (1973: 22) synonymized it. This genus also includes the Oligocene species *N. simonsi*, described by Wood (1968) as *Paraphiomys simonsi*. We divide the Petromuridae into three subfamilies: the Petromurinae for *Petromus*; the Phiomyinae for *Phiomys*, *Paraphiomys*, *Kenyamys*, *Simonimys* and *Epiphiomys*; and the Diamantomyinae

for *Metaphiomys*, *Diamantomys* and *Pomonomys*. The Myophiomyidae include two subfamilies: the Myophiomyinae for *Myophiomys*, *Elmerimys*, *Andrewsimys*, and *Phiomyoides*; and the Phiocricetomyinae for *Phiocricetomys*. We feel no conviction that these last two subfamilies deserve to be united at the familial level.

We assume that Lavocat's citation (1973: 163) of an undescribed Eocene genus from Pakistan that might be a thryonomyoid was a reference to one of the forms described by Hussain *et al.* (1978), in which case it is a ctenodactyloid and has no bearing on the problem of hystricognath relationships.

APPENDIX 1: LIST OF REFERRED SPECIMENS OF *SALLAMYS PASCUALI*, *INCAMYS BOLIVIANUS* AND *BRANISAMYS LURIBAYENSIS*

Sallamys pascuali. Eleven specimens in the Princeton collection: PU nos. 20906, a fragment of the right maxilla with P^4–M^1; 20907, a portion of the right ramus with part of the incisor and P_4–M_2; 20908, a portion of the right ramus with part of the incisor, roots of P_4 and much worn M_{1-2}; 20909, a fragment of the right ramus with part of the incisor and dm_4–M_2; 20910, a fragment of the right ramus with M_1 and the roots of P_4; 20911, a fragment of the left ramus with M_2 much worn and roots of P_4–M_1; 20912, a portion of the left ramus with part of the incisor and M_{1-2}; 20913, a portion of the left ramus with a broken incisor and the roots of P_4–M_3; 20982, an upper left molar, probably LM^1; 21727, a portion of the right ramus with M_{2-3} and the roots of P_4–M_1; and 21950, part of the right ramus with M_{1-2}. PU nos. 20908 and 20911 could be parts of one individual.

Incamys bolivianus. One hundred forty specimens in the MNHN, Princeton and MACN collections, as follows: SAL 119, Ldm^3–M^1; SAL 120, (R or L?) P^4–M^2; SAL 121, (R or L?) P^4; SAL 122, (R or L?) P^4; SAL 123, (R or L?) P^4; SAL 124, Ldm_4–M_2; SAL 125, Rdm_4–M_2; SAL 126, RP_4–M_1; SAL 127, LP_4; SAL 128, (R or L?) dm_4–M_3; "33 mandibules plus ou moins complètes SAL 129 à SAL 161" (Lavocat, 1976: 50); SAL 162, partial skull, and SAL 162A and 162B, associated rami of the lower jaw, type of *I. pretiosus*. The Princeton material includes PU no. 21726, skull and incomplete mandible found in connection, skull somewhat distorted but nearly complete, damaged in the orbital region and lacking the tips of the premaxillaries and incisors, the arches and antorbital bars, and part of the right bulla, mandible incomplete posteriorly on both sides and lacking tips of incisors and symphysis, but including all deciduous and permanent molars; PU no. 21945, skull with articulated mandible, missing the tip of the snout and left zygomatic arch, the ventral part of the mandible and the angles, but otherwise nearly complete and uncrushed; PU no. 20944, the anterior part of a skull, damaged and lacking all the cheek teeth; and 91 other specimens—PU no. 20953, incomplete premaxilla with broken I^1; PU no. 21728, maxilla with LM^{1-3} and partially erupted LP^4; PU nos. 20929, 20938–9, 20947, 20950–2, 20954–68, 20979–80, 21949, 21956, 21958–9, 21970–1, 21982 and 21985, fragmentary maxillae and isolated upper cheek teeth; PU nos. 20916–28, 20930–7, 20940–3, 20945–6, 20948–9, 20969–78, 20981, 21729–31, 21735, 21941, 21946–7, 21952–4, 21957, 21981, 21983 and 21987, fragmentary lower jaws and isolated lower cheek teeth. Of these, PU nos. 20965 and 20979, R and L P^4, may represent one individual; PU nos. 20954 and 20960, R and L P^4–M^2, another; and PU nos. 20958 and 20963, R and L P^4, a third. As indicated above (p. 429), MACN no. A 52-113, an isolated upper cheek tooth, identified by Wood and Patterson (1959: 362–4) as "?dasyproctid gen. et sp. indet.," belongs here.

Branisamys luribayensis. Thirty-one specimens in the MNHN and Princeton collections, as follows: a partial mandible with RP_4–M_1 and LM_{1-3} (SAL 103) was referred here by Hoffstetter and Lavocat (1970). Lavocat (1976: 33) referred SAL 104, (R or L?) M^{1-2}; SAL 105, fragment of the ramus with RP_4–M_3; SAL 106, erupting P_4 and M_1 (R or L?); SAL 107, LM_1 and posterior part of Ldm_4; SAL 108–115, eight partial mandibles with teeth; and SAL 116, jaw fragment (R or L?) with roots of cheek teeth. Our material consists of PU no. 20914, incomplete anterior half of a skull with broken incisors and damaged LP^4–M^3; PU no. 21960, a partial snout with both incisors, showing the naso-frontal contact and damaged ventral and lateral areas back to near the rear of the diastema; PU nos. 21732 and 21733, right and left maxillary fragments with little worn P^4–M^1, almost certainly representing the same individual; PU no. 21943, maxillary fragment with worn and broken RP^4–M^3; PU no. 21955, maxillary fragment with Rdm^4–M^1 and the root of dm^3; PU no. 20915, small fragment of maxilla with LP^4; PU no. 21944, mandible with RM_{1-3}; PU no. 21951, fragmentary mandible with RP_4–M_2; PU no. 21980, fragment of right mandible with P_4; PU no. 21987, fragmentary mandible with Rdm_4–M_1; PU no. 21986, isolated LM_2; PU no. 21734, fragment of mandible with RM_3 and damaged incisor; and PU nos. 21978, 21979, 22172 and 22173, fragmentary mandibles with incisors and roots of the cheek teeth. GB 014, Ldm_4, the type of *Villarroelomys bolivianus*, belongs here.

APPENDIX 2 (BY B.P.): VALIDATION OF *ACARECHIMYS*

The name *Acarechimys* was quoted ex ms. by J. L. Kraglievich (1965: 258) and credited to Patterson. The formalities, which it becomes necessary to supply, are as follows.

Acarechimys Patterson (*in* J. L. Kraglievich, 1965)

Diagnosis. Cheek teeth somewhat higher crowned than in *Protacaremys.* Upper molars with transverse lophs; anterolophs and posterolophs of M^{1-2} closely approaching buccal extremities of proto- and metalophs, uniting early in wear; posteroloph of M^3 reduced. Dm^4 tending toward reduction and loss of metaloph. Lower molars with variable metalophid, interrupted or absent in M_{1-2}, absent or interrupted in M_3, metaflexid deeper than mesoflexid in M_3. Dm_4 with metalophid united to metaconid or, rarely, falling short if it; anterior fossettid usually divided by anteroposteriorly or obliquely aligned neolophid. Masseteric crest stronger and more projecting than in *Protacaremys.*

Distribution. Santacruzian Miocene, Patagonia.

Type Species. Acaremys minutus Ameghino 1887 (Synonym: *Stichomys gracilis* Ameghino 1891).

Referred Species. Acaremys minutissimus Ameghino 1887 (Synonyms: *Stichomys diminutus* Ameghino 1891, *Sciamys tenuissimus* Ameghino 1894 and, provisionally, *Stichomys constans* Ameghino 1887).

The generic name commemorates the long-standing confusion of early octodontids (as "Acaremyinae" or "Acaremyidae") and echimyids, which is reflected in the synonymy above.

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ADDENDUM (by A.E.W.)

Since this manuscript was sent to the printer, several papers pertinent to our discussion have been received.

Evidence of the distinct nature of the Tertiary Middle American rodent fauna (p. 457) is given by Slaughter (1981), who described a rather distinctive new genus of geomyoid from the Miocene of Texas and Panama. He suggested (1981: 114) "that the Coastal Plain, perhaps all the way to Florida, was a northern portion of the Central American tropical biotic province . . . ."

Presence of the Hesperomyinae in Chihuahua in the early Pliocene (Jacobs and Lindsay, 1981), well before their earliest known occurrence in South America, should put an end to suggestions that they had an African origin. This also adds to the documentation of the Middle American fauna.

Vucetich (1980: 99–105) redescribed *Simplimus indivisus* and agreed with Fields that it is a dinomyid (see above, p. 427). She differs somewhat from our caviomorph classification. She transferred (1980: 10) the Dasyproctidae to the Cavioidea, as do we, but left the Dinomyidae in the Chinchilloidea, and did not mention the Cuniculidae. We continue to believe (see above, p. 511) that the Dasyproctidae and Dinomyidae belong together, in whatever superfamily they are placed.

Parent (1980: 166–169) described the middle ear of erethizontids. He concluded (1980: 253) that they were quite distinct from the other caviomorphs and that they perhaps diverged from the Caviomorpha before their arrival in South America. He also noted (op. cit.: 255) that the erethizontid ear region is the most primitive among all the hystricognaths he studied (which did not include the Eocene franimorphs *Reithroparamys* and *Protoptychus*). I believe that this monograph demonstrates the correctness of our interpretation (see above, p. 482) that he has shown that it would be impossible to derive the Erethizontidae from any Old World hystricognath. His conclusions support those we present above (p. 509). As previously, we accept the thesis that the Hystricognathi are a natural group.

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